

*The
Beagle*

RECORDS
OF THE
MUSEUMS
AND
ART GALLERIES
OF THE
NORTHERN TERRITORY

Volume

14

October

1993



The BEAGLE, Records of the Museums and Art Galleries of the Northern Territory

(formerly "Records of the Northern Territory Museum of Arts and Sciences")

ABSTRACTED IN ZOOLOGICAL RECORD AND BIOSIS

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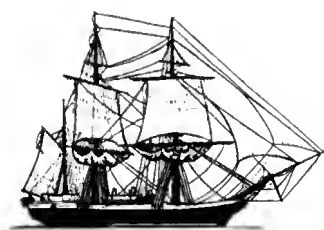
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ISSN 0811-3653

Printed by the Government Printer of the Northern Territory



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THE FOSSIL FLORA OF MELVILLE ISLAND, NORTHERN AUSTRALIA

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ABSTRACT

Twenty-seven angiosperm taxa and two conifers are described from the Van Diemen Sandstone of Melville Island, Northern Territory. The angiosperms include *Brachychiton*, *Grevillea*, *Melaleuca*, and probable Cunoniaceae. The conifers are *Araucaria* and an unidentified genus of the Cupressaceae. Floristics and physiognomy suggest the climate was neither megathermal nor microthermal but that rainfall may have been seasonal. Two distinct assemblages are present, one from clay-rich mud, the other from sandier lithologies. The age of the Van Diemen Sandstone, which was probably deposited by a perennial sinuous river, is not known more precisely than Tertiary, but is suggested here to be Paleogene.

KEYWORDS: Plant macrofossils, Tertiary, *Araucaria*, Proteaceae, Paleogene

INTRODUCTION

Almost all the knowledge of Australia's vegetation history during the Tertiary, when angiosperms had reached the world-wide prominence they have today, comes from the south-eastern corner of the country. A few localities are known along the southern edge of the mainland, in Western Australia, and in southern and central eastern Queensland. There are even a few bore hole samples with fossil pollen from central Australia. But the vast area that remains - essentially the northern half of Australia - is a virtual blank in time for over 80 million years. This is frustrating, for although the record elsewhere is excellent, it is half a continent away and almost certainly would have lain in a completely different climatic belt. Palaeontologists are naturally curious to know what was happening in the presently tropical latitudes as well as the temperate ones. This gap in the record places great importance on the one locality that is known - Cape Van Diemen at the north-west tip of Melville Island, which lies north of Darwin (Fig. 1). Fossils from this location were first described by White (1974), and from the results of a brief collection made by D. Bowman (Pole and Bowman 1996). The fossils are poorly preserved, lacking organic preservation and with little chance of

including pollen, but this was to be expected in a region enduring a hot, monsoonal weathering regime. While not expecting any miracles of preservation, intensive collection would likely add more taxa, more complete specimens, perhaps more localities, and maybe indicate something in the geology that would help to date the deposit. This stimulated support for a major expedition which formed the basis of this paper.

GEOLOGY

The Van Diemen Sandstone forms approximately 17.5 m high coastal cliffs of the eastern side of Cape Van Diemen. The sediments are essentially flat-lying, though there may be some gentle warping. The top two or three metres are dark red and form the uppermost part of a lateritic weathering profile. Slope-wash of this red material frequently obscures parts of the cliff and makes continuity of bedding difficult to observe.

A schematic indication of the geology is shown as Figure 2. The lower ten metres or more are predominantly formed of tabular cross-bedded sands. The apparent direction of flow of most beds in the cliff face is from south east to north west. Exposures at right angles to the cliff line show most movement

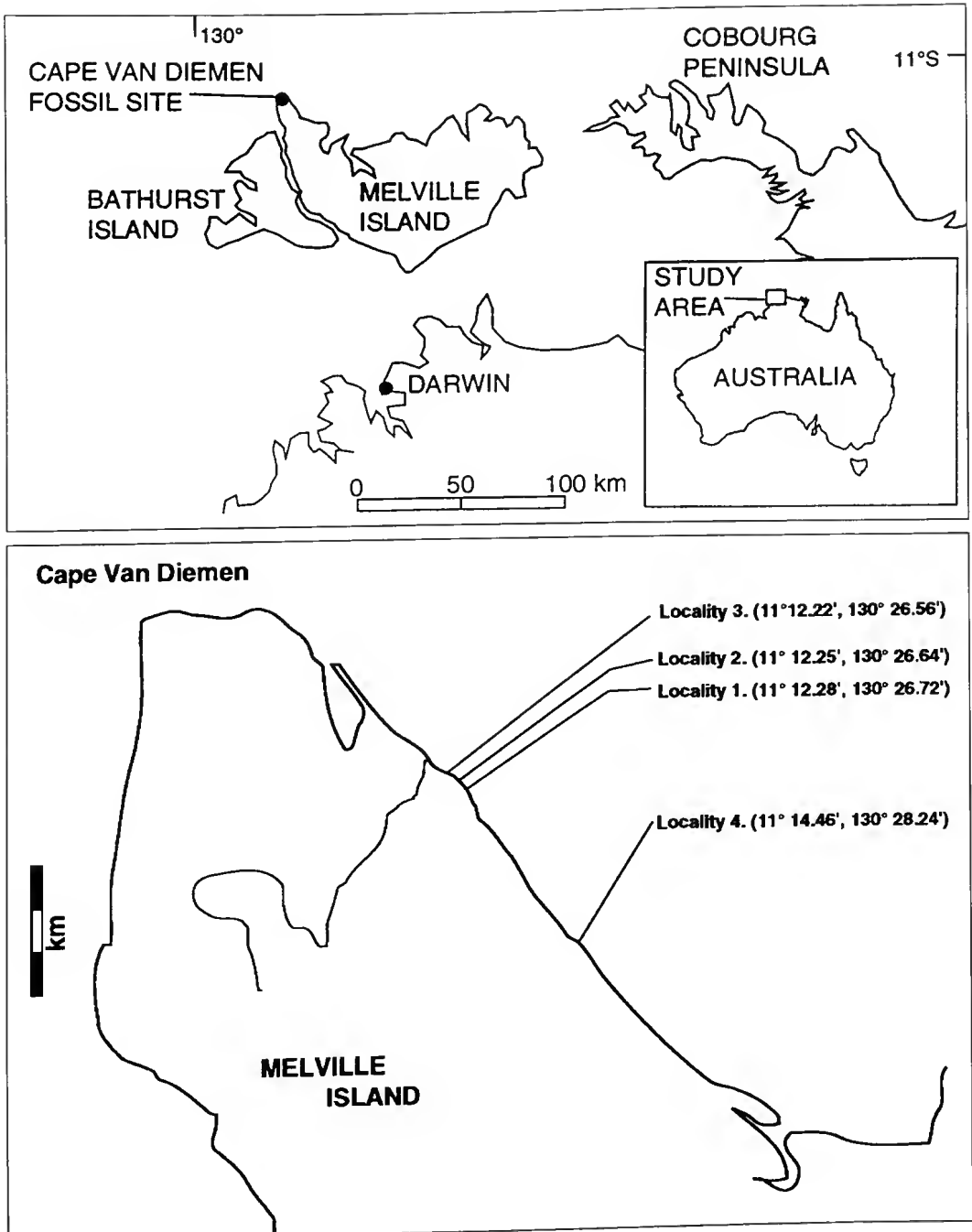


Fig. 1. Locality map.

was away from the coast, i.e., a south-westerly direction. This indicates the dominant true direction of flow was generally westerly. One bed had overturned forsets.

Higher in the cliff, discrete lenoid bodies of sediment contain the bulk of the plant

fossils. The lenses appear to be shallow channels which were cut into the underlying sandstone, though in detail, a clear erosional base is not always clearly seen. It was not practical to collect fossils directly from these lenses (extraction was too hard) but boulders forming the talus below were readily

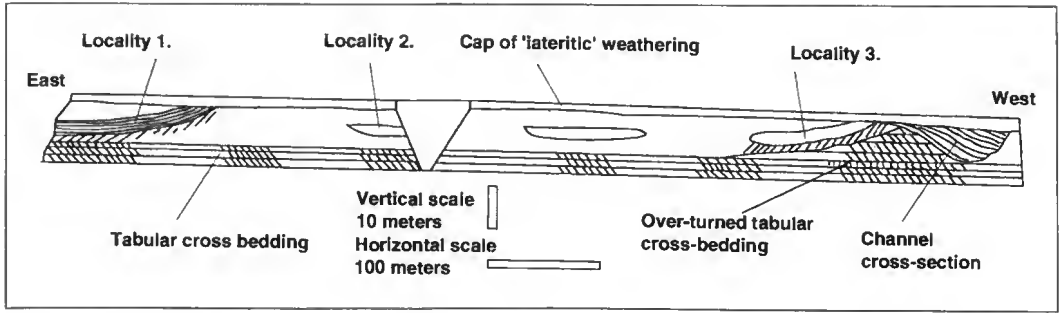


Fig. 2. Schematic geology.

accessible and clearly derived from the lenses. Collecting concentrated on four lenses, designated localities 1-4. Lenses 1-3 were numbered in a westerly direction. Locality 4, much further to the east, was discovered later. The assemblage described in Pole and Bowman (1996) comes from Locality 3. Within Locality 1, several boulders had a distinct lithology of soft, fissile, purple-coloured mud. Fossils are abundant in the 'purple mud' facies and fossils from this facies are treated as a separate assemblage. Other sediment coming from Locality 1, and from the other localities was heterogeneous, but generally much sandier.

To the west of Locality 3 a clear cross-section of a fluvial channel can be seen, which has been filled by lateral accretion. Another may exist between Locality 2 and 3. Fine-grained intraclast pebbles are common as lag accumulations at the base of the channels and at the base of many of the forsets.

These appear to be fluvial sediments deposited by a large, highly sinuous river with relatively continuous flow. This interpretation is based on:

- a) the existence of the channel or channels, which are at right angles to the tabular cross-bedding at the base, indicating the change in flow direction as a fluvial meander cut its way into older channel sediments;
- b) the lensoid bodies containing the plant fossils, which suggest cut-off meanders, or 'ox-bow' lakes;
- c) the large amount of 'claystone' lag associated with channel bases and the bases of forsets. This suggests a large amount of overbank material and

constant reworking of the floodplain by migrating channels;

- d) there is no evidence of ephemeral flow, which would be more typical of less sinuous, or braided fluvial systems, although the over-turned forsets do indicate that flow may have increased suddenly at times.

METHODS

This paper is the result of three days collecting on Melville Island by ten people in September 1994. The island was accessed by boat. Collecting was carried out using rock hammers, picks, and a pneumatic drill. Specimens were further exposed, where necessary, by a compressed-air powered chisel in the Department of Botany, University of Tasmania. Leaves were illustrated by tracing with a Nikon Profile Projector and then redrafting on architectural film, and by photography. The sediments are too deeply weathered to preserve cuticle or palynomorphs. All material collected on this expedition was catalogued and stored in the Museum and Art Gallery of the Northern Territory (numbers prefixed with 'P'). Specimens prefixed with SB were referred to in Pole and Bowman (1996), and are stored in the same place under P98123.

After grouping all specimens into taxa, and description, identification was attempted based on leaf architectural characters (following the terminology of Hickey 1973; Dilcher 1974; and with some modifications by Pole 1991) and using herbarium material and published illustrations. The formal taxonomy, including taxa described by Pole and Bowman (1996) is presented after the

following discussion on identification. To shorten descriptions, only instances where 'development' (sensu Pole 1991) deviates from 'normal', or where it is unclear, are mentioned.

Key indicating basis for angiosperm taxa

- | | |
|--------------------------------------------------------------------------------------|----------------------------------------------------------------------------------|
| 1. Leaves compound or specimen obviously a leaflet 2 | 11. L:W > 8, width < 10 mm .. Entire type A |
| 1. Leaves simple or not obviously leaflets.....7 | 11. L:W > 8, width > 10 mm ... Entire type F |
| 2. Unattached leaflet ovate, with curved, asymmetrical base ... Compound leaf G | 11. Shape elliptical (L:W about 2) Entire type B |
| 2. Leaflets attached to form compound leaf 3 | 11. Shape oblong Entire type D |
| 3. Leaf trifoliate Compound leaf E | 11. Shape obovate, with tapering base Entire type E |
| 3. Leaf pinnately compound 4 | 12. Teeth recumbent with prominent glandular apex Toothed Margin Type A12 |
| 4. Leaflets petiolate Compound leaf B | 12. Teeth without prominent glandular apex 13 |
| 4. Leaflets sessile 5 | 13. Shape lanceolate or very narrow elliptic (L:W > 8) 14 |
| 5. Leaflets longer than 100 mm Compound leaf A | 13. Shape narrow ovate or wide elliptic (L:W < 3) 16 |
| 5. Leaflets shorter than 100 mm 6 | 14. Teeth prominent, about 1.5 mm high Toothed Margin Type J |
| 6. Leaflets with small teeth Compound leaf D | 14. Teeth low, 1 mm high or less 15 |
| 6. Leaflets with large teeth Compound leaf C | 15. Lateral venation high angle, very closely spaced Toothed Margin Type F |
| 6. Leaflets with deep sinuses Compound leaf F | 15. Lateral venation low angle, loose, disorganised Toothed Margin Type C |
| 7. Leaves lobed 8 | 16. Major venation externodromous Toothed Margin Type D |
| 7. Leaves entire 9 | 16. Major venation craspedodromous ... 17 |
| 7. Leaves toothed 12 | 16. Major venation unclear, apex bluntly triangular Toothed Margin Type G |
| 8. Leaves deeply dissected, pinnatisect <i>Grevillea</i> | 18. Teeth large, triangular Toothed Margin Type B |
| 8. Leaves deeply bilobed cf. <i>Dilobeia/Liriodendrites</i> | 18. Teeth small, erect Toothed Margin Type E |
| 8. Leaves with five radiating lobes <i>Brachychiton</i> | |
| 9. Major venation of about three orders of (apparently) longitudinal veins 10 | |
| 9. Major venation not strong enough to be seen clearly..... 11 | |
| 9. Major venation pinnate, 3-4 laterals each side, wide elliptic Entire Type C | |
| 10. Shape lanceolate <i>Melaleuca</i> | |
| 10. Shape ovate <i>Smilax</i> | |

SYSTEMATICS

A complete list of all Melville Island specimens follows. This includes those described in Pole and Bowman (1996). These are not redescribed unless significant new material was found.

Possible fern

Branching shoots with leaves flattened into one plane on either side of an axis were dominant at Locality 4 (Fig. 3). The leaves are imbricate and have an open dichotomous venation. This suggests a fern, or fern-like plant. The superficial resemblance to

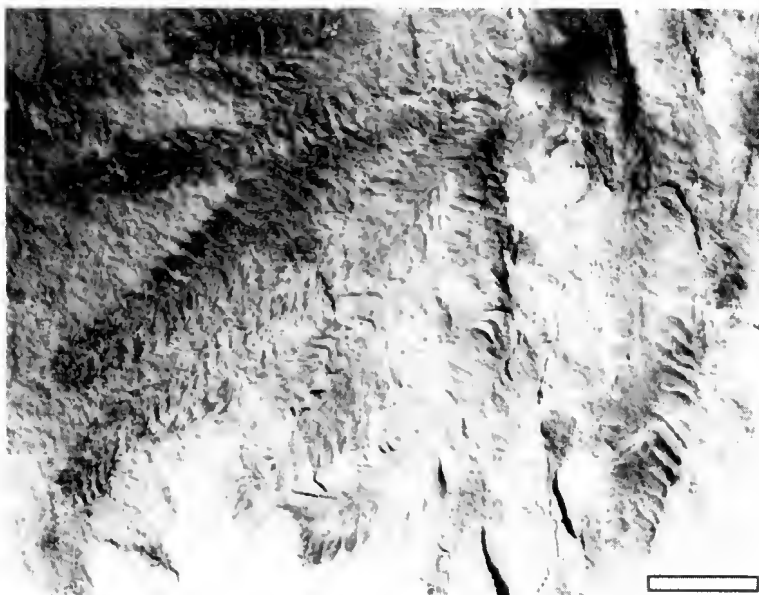


Fig. 3. ?Fern. P94327 (scale = 10 mm).

lycopods and conifers is ruled out by the venation, however placement within some extinct gymnosperms like *Bennettitales* is not ruled out.

?Fern
(Fig. 3)

Reference specimen. Locality 4: P94327.

Araucariaceae

Several shoots and a single detached leaf clearly belong to *Araucaria* (Fig. 4). At least two ovuliferous cone/seed complexes were recovered which presumably belong with the foliage, one of these has thin lateral wings indicating *Araucaria* section *Eutacta*. Three specimens which appear to be elongate structures of small, helically-disposed scales, may be male cones of *Araucaria*.

***Araucaria* sp.**
(Fig. 4)

Referred material. Locality 1: shoots P94217, P94219, P94220, P94224; leaf P94223; ovuliferous cone scale: P94216, P94218; ? male cones P94221, P94222. Locality 3: detached leaf P94303; ovuliferous cone scale P94300, P94311.

Description. Shoots with triangular, slightly flattened, scale-like leaves. Ovuliferous cone scale with thin lateral wings.

Cupressaceae

An additional specimen of a shoot with opposite-decussate leaves described as Cupressaceae by Pole and Bowman (1996) was recovered.

Cupressaceae gen. et sp. indet.
(Pole and Bowman 1996)

Referred material. Locality 1: P94117, P94191-P94193. Locality 2: P94262. Locality 3: SB916, SB917, SB973.

Proteaceae

Several deeply dissected leaves regarded by White (1974, 1976) and Pole and Bowman (1996) as *Grevillea* were recovered (Fig. 5). The new material suggests more than one species may be represented, but there are not enough specimens to confirm this.

Many more specimens of *cf. Dilobeia* (Pole and Bowman 1996) were recovered including one nearly perfect example (Fig.

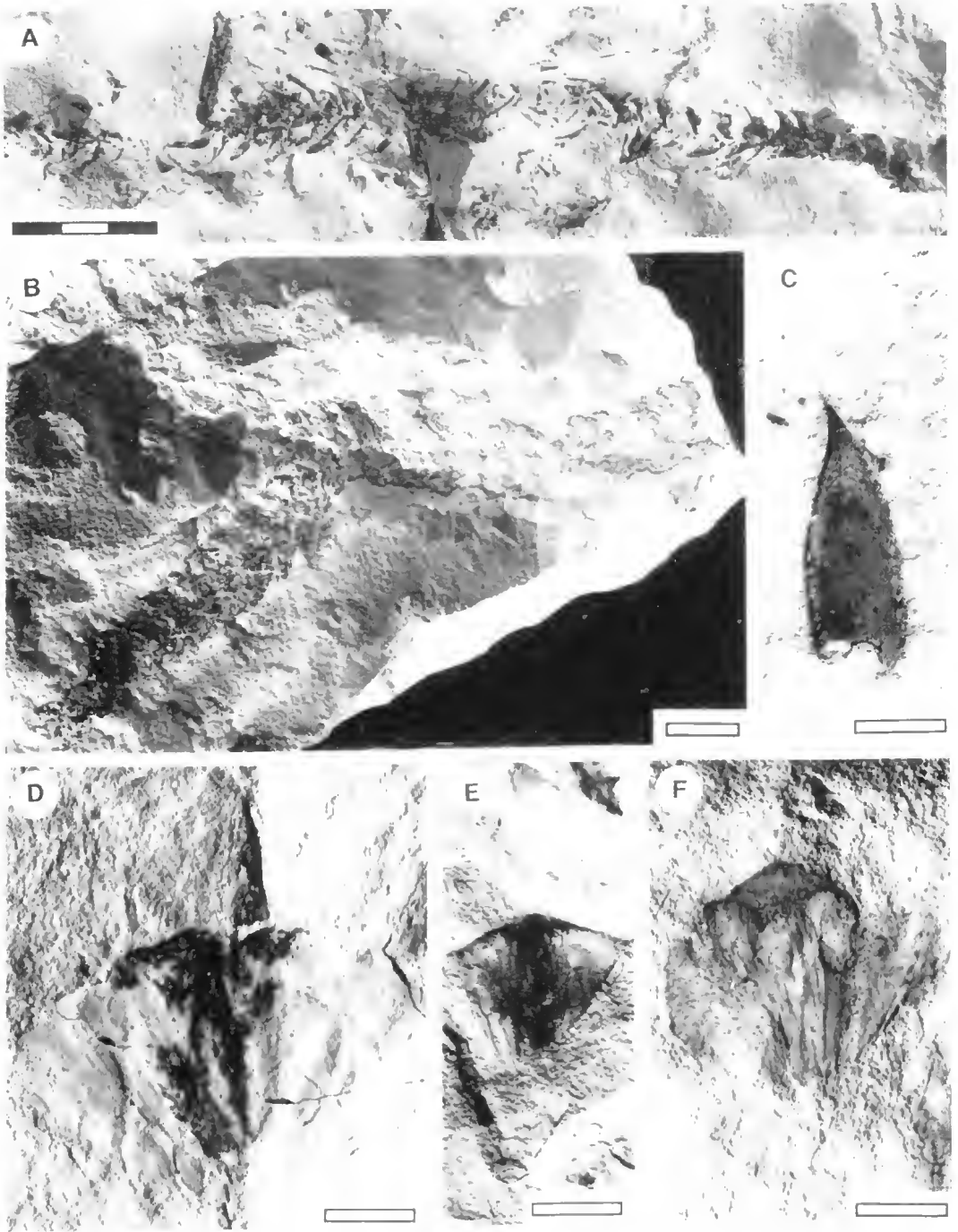


Fig. 4. *Araucaria* sp. A, shoot, P94224 (scale = 30 mm); B, shoot, P94219; C, leaf, P94303; D, ovuliferous scale, P94311; E, ovuliferous scale, P94218; F, ovuliferous scale, P94216 (B-F, scale = 10 mm).

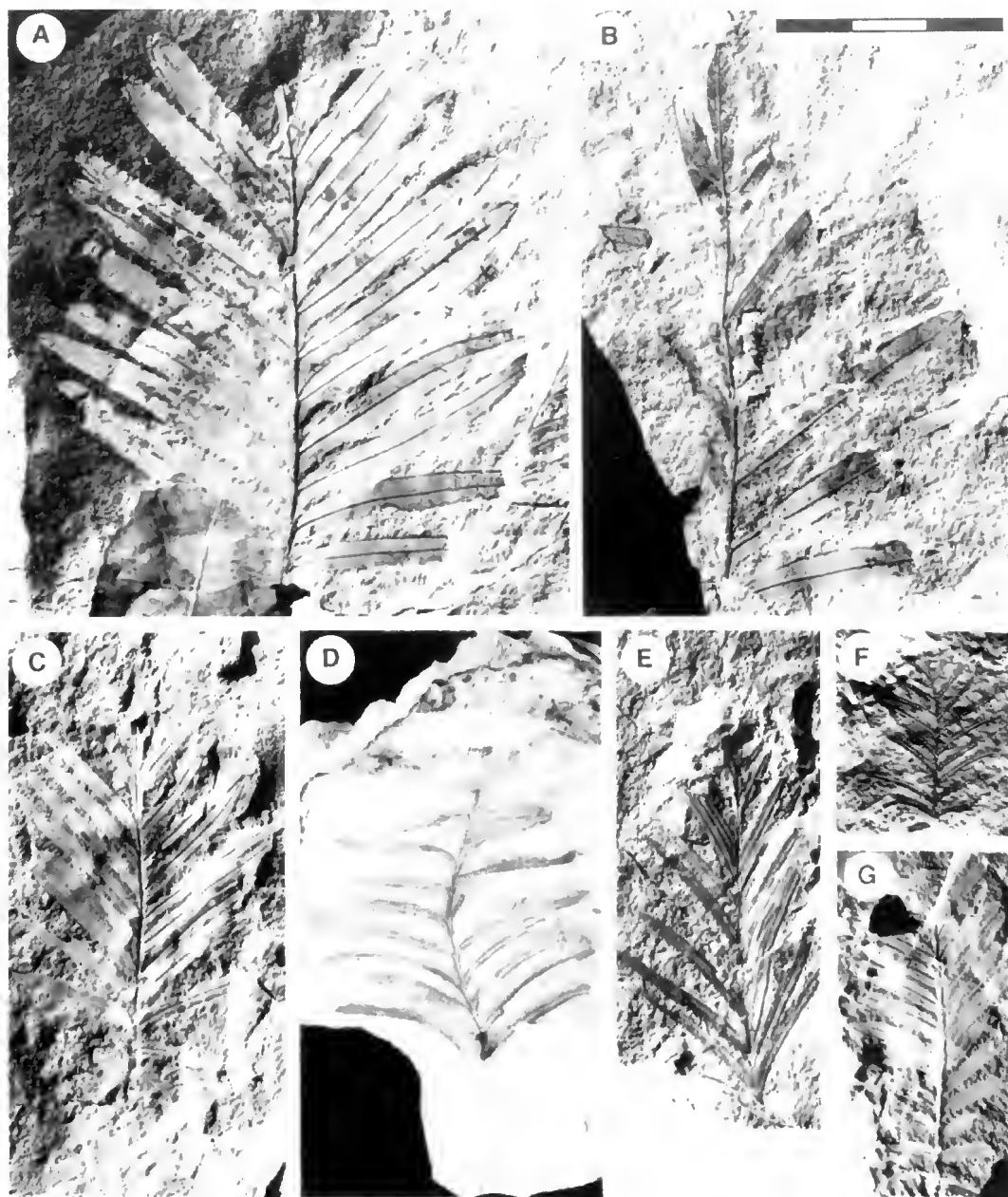


Fig. 5. *Grevillea* sp. cf. *G. whitiana*. A, P94122; B, P94125; C, P94169; D, P94167; E, P94271; F, P94270; G, P94101 (scale = 30 mm).

6). The extinct genus *Liriophyllum* Lesq. emend. Dilcher and Crane (1984) from the mid Cretaceous of the USA is rather similar in having a bilobed lamina but was not discussed by Pole and Bowman (1996). It differs from the Melville Island fossils in having a stout midrib extending to the base

of the sinus and forking into two prominent veins, distinct from the secondary veins below, which form the leaf margin typically for about 0.3–0.16 of the lobe length. Above this point the lamina arches away from the vein into the sinus and broadens distally to form each lobe (Dilcher and Crane 1984). In

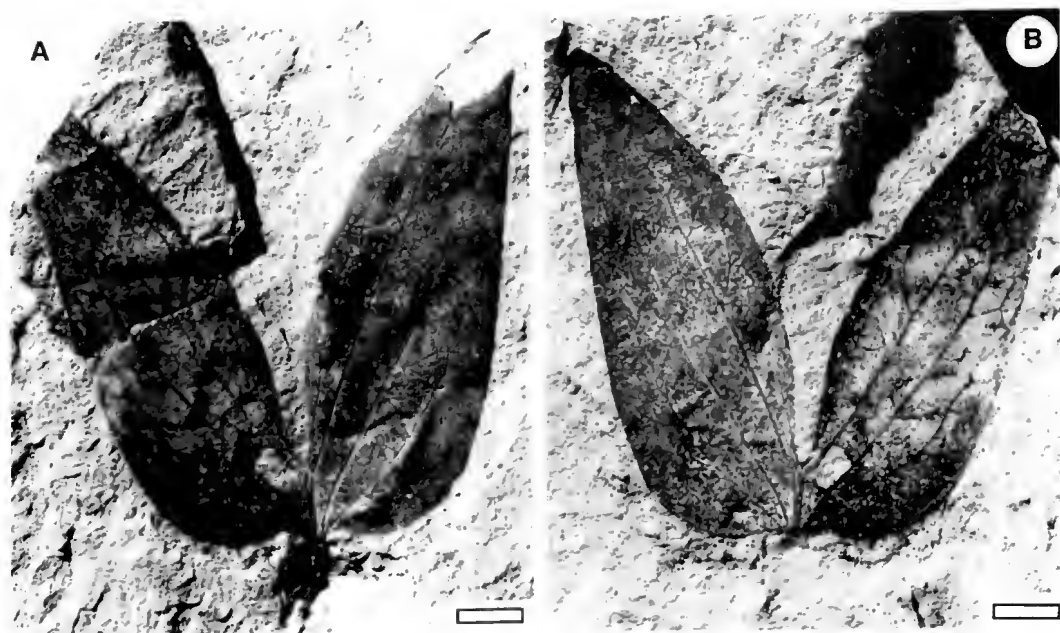


Fig. 6. *cf. Dilobeia/Liriodendrites*. P94297, A, part; B, counterpart (scale = 10 mm).

the new fossils, the midrib is quite reduced when it reaches the sinus, there is no sign of it forking, and there is no pronounced arching of the lamina into the sinus (forming counter-external veins *sensu* Pole 1991). In a recent paper, Johnson (1996) described a new bilobed leaf genus, *Liriodendrites*, from the latest Cretaceous of the USA. The description of this genus clearly covers the Melville Island fossils. However, while *Liriodendrites* was assigned to the Magnoliales, and perhaps to the Magnoliaceae, the generic description would also include the extant Proteaceae genus *Dilobeia*, to which the Melville Island fossils have been compared. This raises a taxonomic problem—whether to continue to refer to the new fossils informally as *cf. Dilobeia*, or to place them in the genus *Liriodendrites*, which, if the American fossils are correctly placed in the Magnoliales, is not a natural group. My taxonomic philosophy is not to formally use genera which are not natural. The Melville Island leaves will continue to be referred to informally as *cf. Dilobeia/Liriodendrites*.

Grevillea sp. *cf. G. whitiana*
(Pole and Bowman 1996).
(Fig. 5)

Referred material. Locality 1: P94101, P94104–P94106, P94167–P94175. Locality 2: P94261, P94270, P94271, P94274. Locality 3: P94122, P94123, P94125, P94314–P94317, P94324, P94325, SB945, SB962, SB966, SB967.

Grevillea sp. *cf. G. longifolia*
(Pole and Bowman 1996)

Referred specimen. Locality 3: SB943.

Grevillea sp. *cf. G. dryophylla*
(Pole and Bowman 1996)

Referred specimen. Locality 3: SB955.

cf. Dilobeia / Liriodendrites
(Fig. 6)

cf. Dilobeia (Pole and Bowman 1996)

Referred material. Locality 1: P94102, P94112, P94114, P94145. Locality 2: P94259. Locality 3: P94286–P94297, SB951, SB952, SB1048.

Smilacaceae

Leaves are common in the 'purple mud' facies of Locality 1 which show the typical

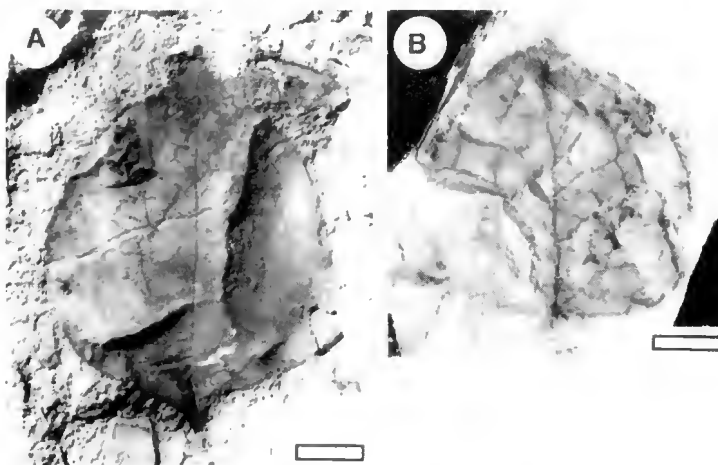


Fig. 7. *Smilax* sp. A, P94143; B, P94135 (scale = 10 mm).

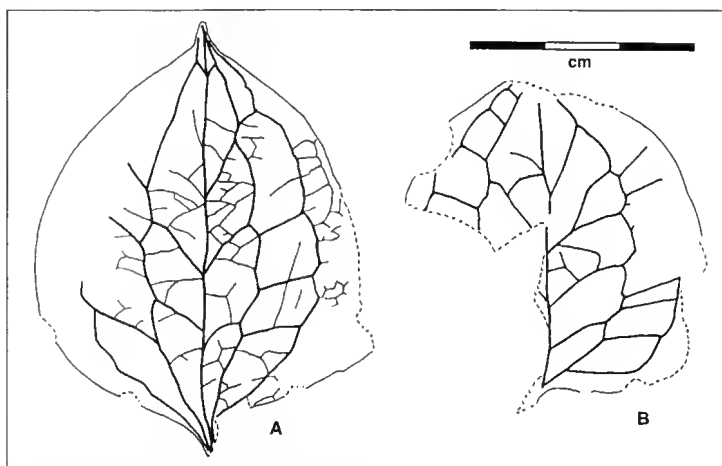


Fig. 8. *Smilax* sp. A, P94135; B, P94143.

venation of the Smilacaceae (Figs 7–8). This consists of a pair of veins which arch directly from the petiole to the apex (these may not be longitudinal veins in the true sense as they may branch downwards, and veins which connect them with the midrib may be of the same order) and these two veins are flanked by a wide looping zone with three well-developed orders of loops. They are identified as *Smilax* by direct comparison with some extant species. There are seven species of *Smilax* in Australia (Conran and Clifford 1986) and more in the areas to the north in the Malaysia-New Guinea region, so it would be premature to identify the fossils

or describe a new species on the poorly preserved material available.

Smilax sp.
(Figs 7–8)

Reference specimen. Locality 1: P94143.
Referred material. Locality 1: P94129–142, P94151, P94158–P94162, P94182, P94202, P94203, P94205, P94206, P94207, P94210–P94212, P94215.

Description. Leaf size: length 22–65 mm, width 13–58 mm. Leaf shape: simple, wide ovate to very wide ovate (a juvenile

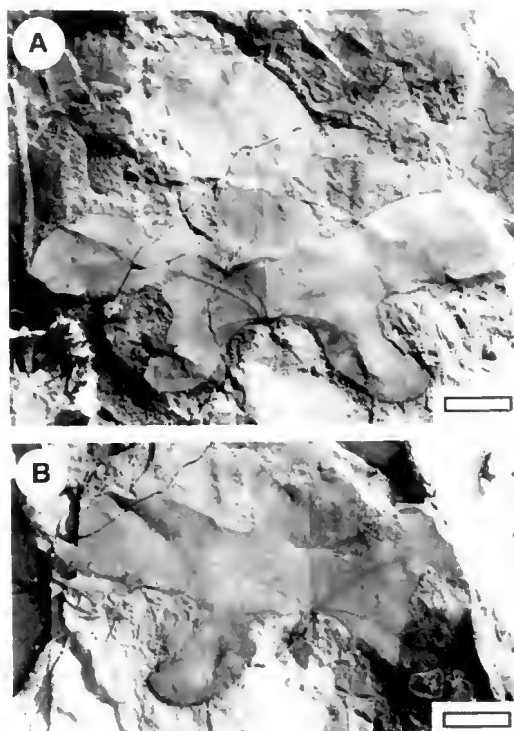


Fig. 9. *Brachychiton* sp. A, P94150, part; B, P94150, counterpart, showing petiole (scale = 10 mm).

specimen is wide obovate); apex rounded but finishing acutely; base rounded but finishing acutely. Margin entire.

Sterculiaceae

Two leaves compare well with some extant species of *Brachychiton* (Figs 9–10). They are palmate with five, entire margined lobes, with basal laterals paired at the base. The petiole is preserved at an angle to the midrib which is taken to indicate presence of an apical pulvinus. In an Australian context, there is little to confuse this form with, although some foreign *Passiflora* are similar. Guymer (1988) monographed *Brachychiton* and the fossils may be compared with his figures. The most similar species, with regard to five lobes which expand slightly in the middle, and a cordate base, is *B. bidwillii* Hook. The Melville Island fossil appears distinct in having a broad sulcus at the base, rather than a sharp notch.

Brachychiton sp. (Figs 9–10)

Reference specimen. Locality 1: P94150.

Referred material. Locality 1: P94144.

Description. Leaf size: length 25–48 mm, lobe width 9–19 mm. Leaf shape: simple, palmatisect (five lobes), apex obtuse, base cordate, sinuses smooth, petiole lying at an angle to midrib, length unknown. Margin entire.

Myrtaceae

Melaleuca sp.

(Pole and Bowman 1996)

Referred material. Locality 1: P94111, P94148, ?P94152, P94154, P94156, ?P94157, P94178, P94180, P94189, P94184, P94204, ?P94208, P94209, P94214. Locality 3: P94307, SB944, SB946–SB949.

? Leguminosae

A possible flattened branch or cladode system, was found (Fig. 11). This is similar to some Leguminosae, but no detailed comparison has been made.

Flattened branch/cladode (Fig. 11)

Reference specimen. Locality 2: P94187.

Description. A central axis, preserved length 65 mm, 2–3 mm wide, with at least three lateral branches. Two of the lateral branches branch again. The structure shows a broad similarity to flattened branches, or cladodes, for instance those found in the Leguminosae. The branches narrow slightly towards the main axis, there is surface detail of longitudinal striations separated by nodes.

Family indet.

Simple Entire Margined Leaves (Figs 12–13)

These have been subdivided quite subjectively, but Entire Margin Type A forms a clear group. These, and perhaps Entire

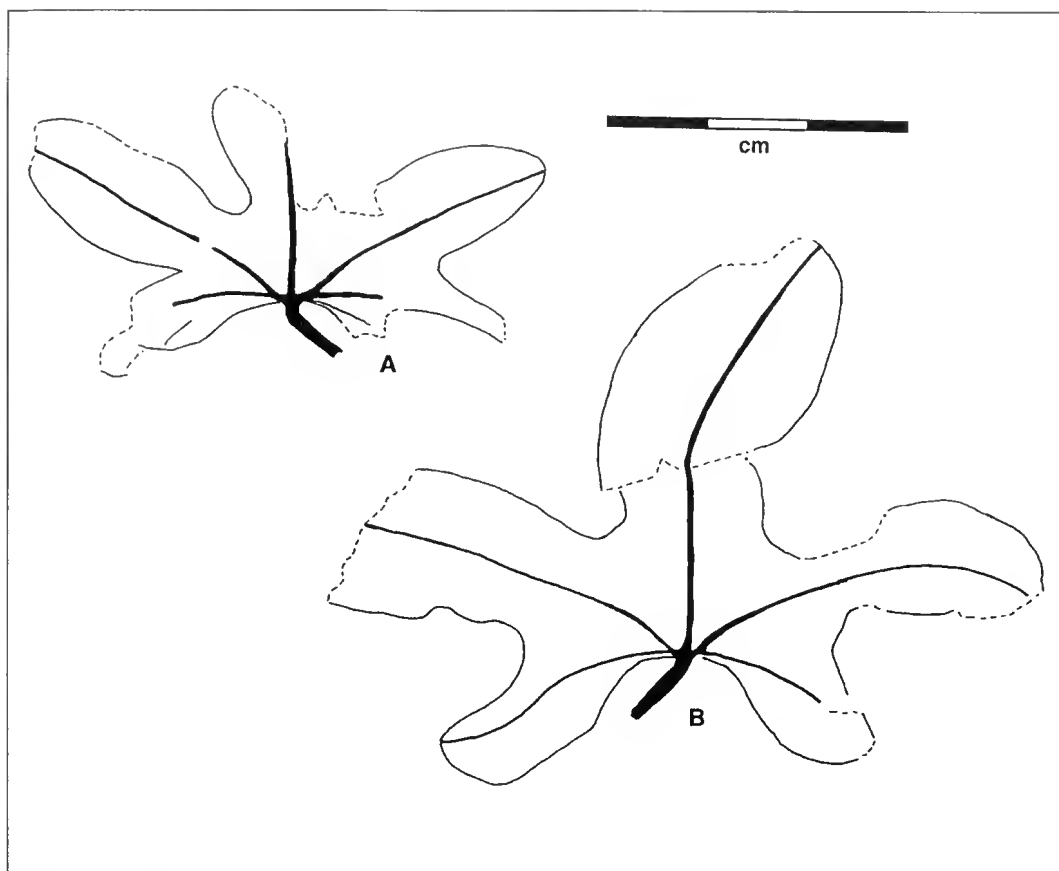


Fig. 10. *Brachychiton* sp. A, P94144; B, P94150.

Margin Type F are putative *Eucalyptus*, but other possibilities exist, such as *Proteaceae*, or even *Podocarpus* in the case of Type A.

Entire Margin Type A (Fig. 12)

Reference specimen. Locality 3: P94302.

Referred material. Locality 1: P94153, P94163, P94181, P94183, P94188, P94194, P94198, P94200, P94201. Locality 2: P94265, P94266. Locality 3: P94301, P94302, P94304–P94309, P94312, P94323.

Description. Leaf size: length 50–120 mm, width 3–5 mm. Leaf shape: simple, lanceolate or very narrow elliptic ($L:W > 8$), apex attenuate, base decurrent, petiole 2–3 mm long. Margin entire. Development unclear.

Entire Margin Type B (Fig. 13A, C)

Reference specimen. Locality 2: P94257.

Referred material. Locality 1: P94238. Locality 2: P94176.

Description. Leaf size: length about 80 mm, 25 mm. Leaf shape: simple, elliptical ($L:W$ about 2), apex acute, base unknown, petiole unknown. Margin entire. Venation externodromous.

Entire Margin Type C (Fig. 13B)

Reference specimen. Locality 1: P94113.

Description. Leaf size: length 21 mm, width 12 mm. Leaf shape: wide elliptic, apex probably obtuse, base obtuse, petiole absent.



Fig. 11. ?Legume/cladode. P94187 (scale = 10 mm).

Margin entire. Venation: externodromous. Three or four laterals on either side of midrib.

Entire Margin Type D (Fig. 13D)

Reference specimen. Locality 1: P94195.

Description. Leaf size: length 66 mm, width 18 mm. Leaf shape: oblong, apex obtuse, base obtuse, petiole unknown. Margin entire.

Entire Margin Type E (Fig. 13E)

Reference specimen. Locality 1: P94196.

Description. Leaf size: length 45 mm,

width 14 mm. Leaf shape: wide elliptic, apex obtuse, base tapered, petiole normal. Margin entire. Development unclear.

Entire Margin Type F (Fig. 13F–J)

Reference specimen. Locality 1: P94194.

Referred material. Locality 1: P94163, P94188, P94194, P94201, P94331.

Description. Leaf size: length 60–>100 mm, width 10–17 mm. Leaf shape: lanceolate, apex probably attenuated, base acute, petiole normal. Margin entire. Development unclear.

Simple Toothed Margin Leaves (Figs 14–16)

Along with *Smilax*, 'Toothed Margin Type A' is the most common leaf type in the purple mud facies of Locality 1. It has a distinct cuneate base, with a moderate length petiole (Figs 14–15). The marginal teeth have distinct glandular tips. Lateral venation is closely spaced, without the typical, well-spaced laterals of most pinnate leaves. *Ceratopetalum* (Cunoniaceae) is a likely identification of the Toothed Margin Type A taxon. A pulvinus is present at the base of the lamina in some species, such as *C. apetalum*, but is absent on the fossil. It is similar in outline to the taxon which White (1974, 1976) identified as *Ceratopetalum* sp., but as well as the teeth being glandular (not observed on the White specimen), the teeth and sinuses in between are more rounded.

Toothed Margin Type E (Fig. 16D) is suggested to be Cunoniaceae. It has craspedodromous venation, where the laterals bisect the margin at the apical edge of small, erect teeth. It may be a leaflet of *Canonia* or *Weinmannia*, but other genera in the family are not ruled out.

Toothed Margin Type A (Figs 14, 15)

Reference specimen. Locality 1: P94233.

Referred material. Locality 1: 94107, P94108, P94116, P94119, P94120, P94121, P94149, P94155, P94164, P94179, P94186,

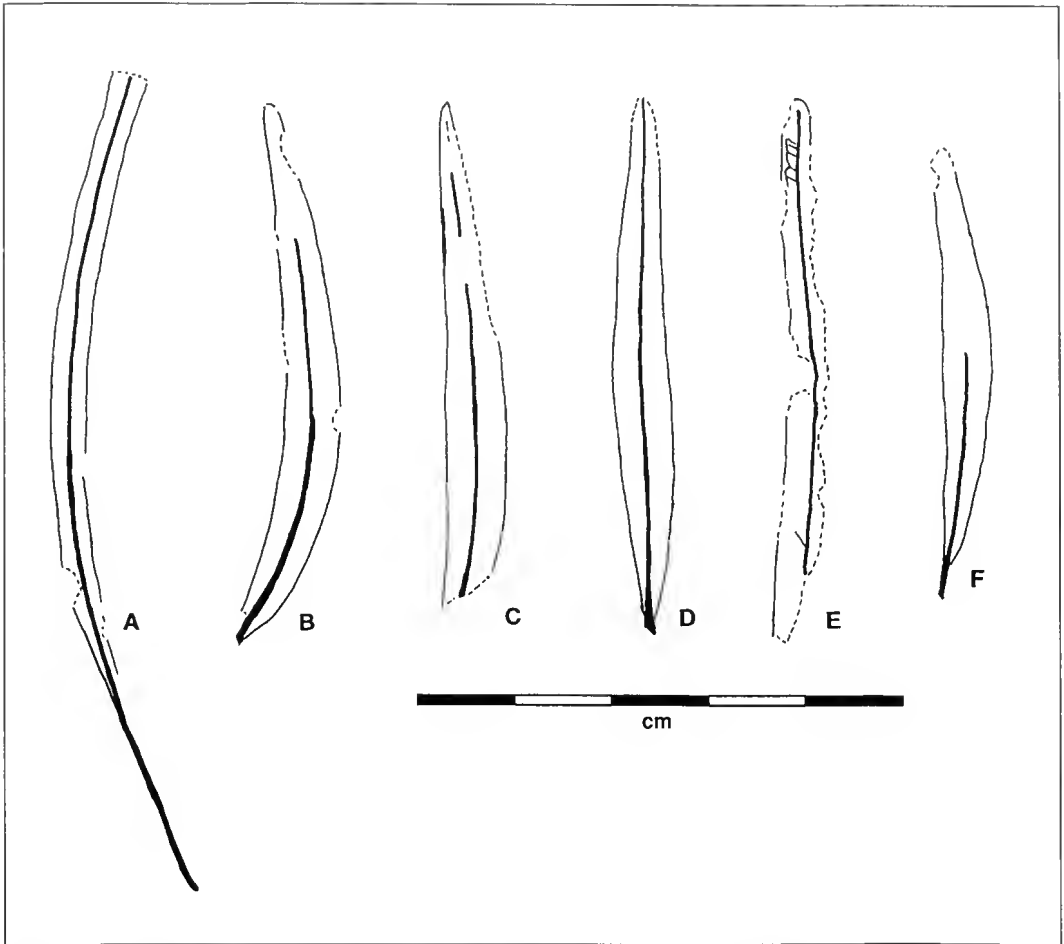


Fig. 12. A, Entire Margin A, P94265; B, Entire Margin A, P94302; C, Entire Margin A, P94304; D, Entire Margin A, P94301; E, Entire Margin A, P94305; F, Entire Margin A, P94312.

P94225–P94237, P94239–P94252. Locality 2: P94260, P94264, P94268. Locality 3: P94321

Description. Leaf size: length 45–160 mm, width 19–84 mm. Leaf shape: lanceolate, apex attenuate, base cuneate, petiole 15–20 mm. Margin non-entire (toothed), with prominent glands at tooth apices, tooth height about 1 mm, recumbent, spacing about 2–5 mm. Venation externodromous.

Toothed Margin Type B (Fig. 16 A)

Reference specimen. Locality 1: P94103.

Referred material. Locality 2: P94254. Locality 3: P94318.

Description. Leaf size: length 18–33 mm, width 5–7 mm. Leaf shape: not clear, possibly a fragment of a simple, lorate or linear leaf, apex unknown, base unknown, petiole unknown. Margin non-entire (toothed), tooth height about 1 mm, inclined, spacing about 4 mm. Venation craspedodromous.

Toothed Margin Type C (Fig. 16B)

Reference specimen. Locality 1: P94197.

Description. Leaf size: length 35 mm, 19 mm. Leaf shape: very narrow elliptic, or

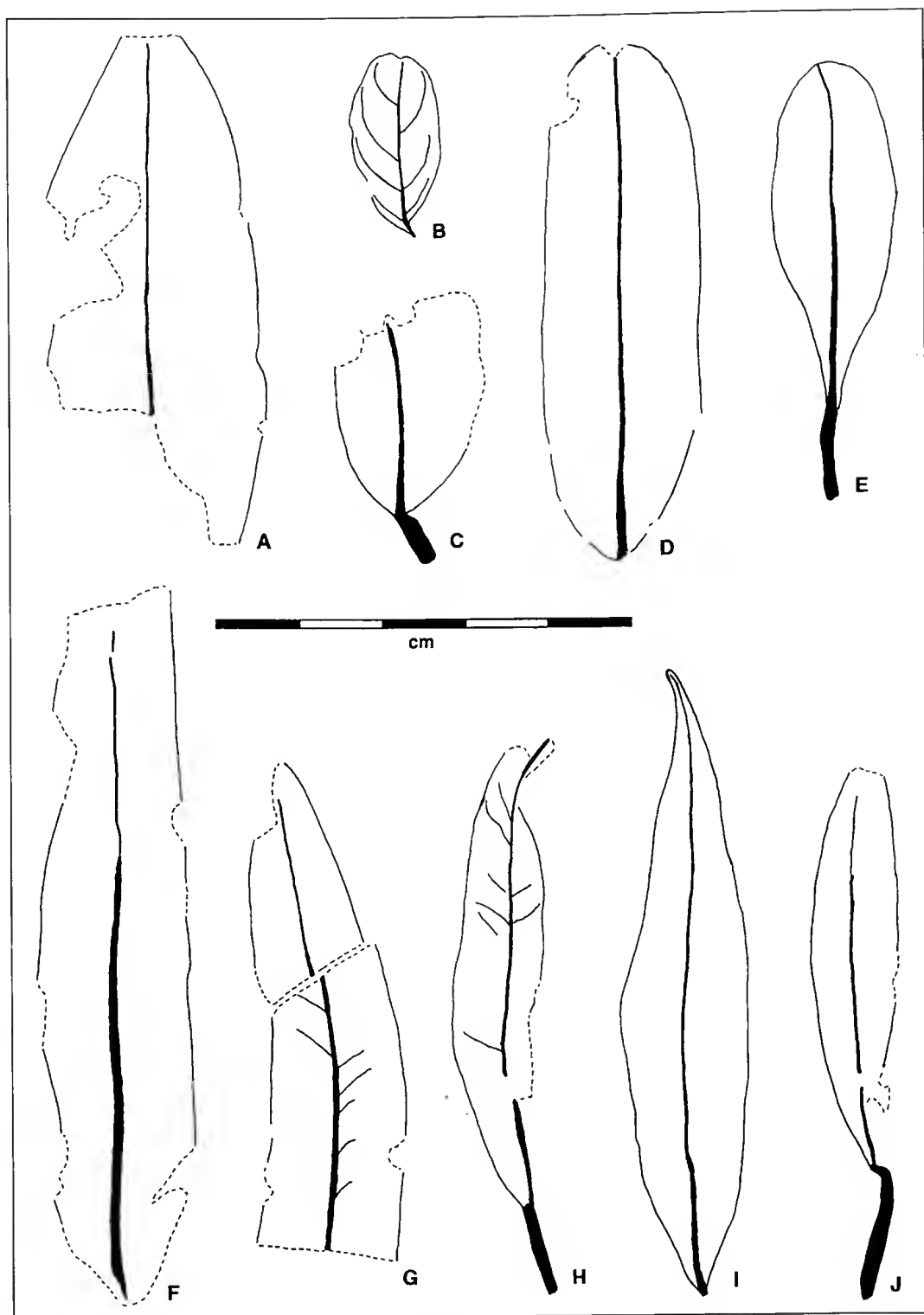


Fig. 13. A, Entire Margin B, P94257; B, Entire Margin B? P94176; C, Entire Margin C, P94113; D, Entire Margin D, P94195; E, Entire Margin E, P94196; F, Entire Margin F, P94163; G, Entire Margin F, P94331; H, Entire Margin F, P94201; I, Entire Margin F, P94194; J, Entire Margin F, P94188.

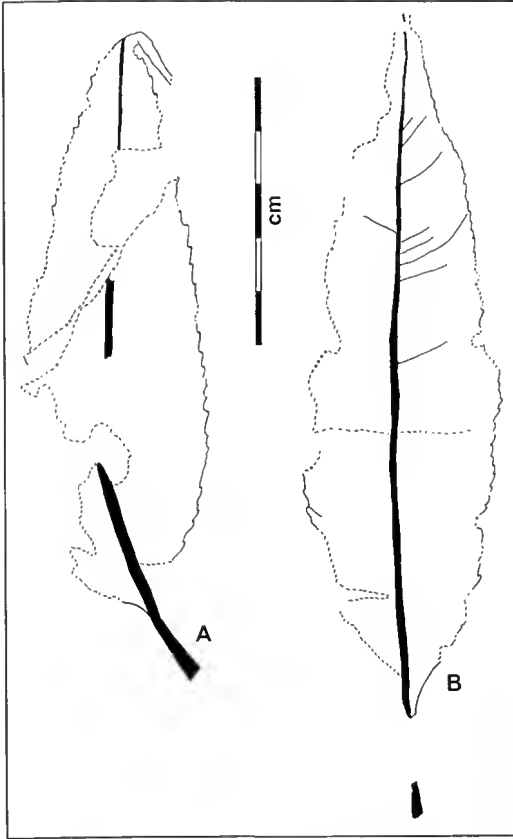


Fig. 14. Toothed Margin A. A, P94233; B, P94234.

narrow oblanceolate, apex unknown, base unknown, petiole 2–3 mm. Margin non-entire (toothed), tooth height 0.5 mm, spacing 2–3 mm. Venation not clear.

Toothed Margin Type D (Fig. 16C)

Reference specimen. Locality 1: P94185.

Referred material. Locality 3: P94319

Description. Leaf size: length 26–35 mm, width 10–16 mm. Leaf shape: narrow ovate, apex acute, base obtuse, petiole absent. Margin non-entire (toothed), tooth height 0.2 mm, spacing 2–3 per mm. Venation externodromous.

Toothed Margin Type E (Fig. 16D)

Reference specimen. Locality 1: P94147.

Referred material. Locality 1: P94115, P94118. Locality 3: P94313, P94322.

Description. Leaf size: length estimated 80 mm, width 32–40 mm. Leaf shape: wide elliptic, apex unknown, base obtuse, petiole absent. Margin non-entire (toothed), tooth height 0.2 mm, erect, spacing about 1–2 mm. Venation craspedodromous.

Toothed Margin Type F (Fig. 16 E, F)

Reference specimen. Locality 3: P94299.

Description. Leaf size: length 105 mm, width 11 mm. Leaf shape: linear or lorate, apex probably attenuate, base unknown, probably decurrent, petiole unknown. Margin non-entire (toothed), tooth height about 1 mm, spacing about 4–5 mm. Venation not clear.

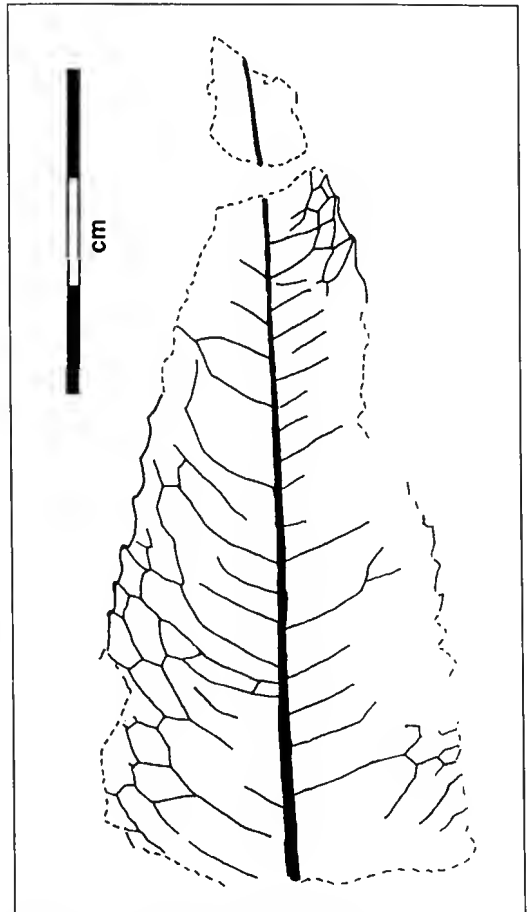


Fig. 15. Toothed Margin A. P94119.

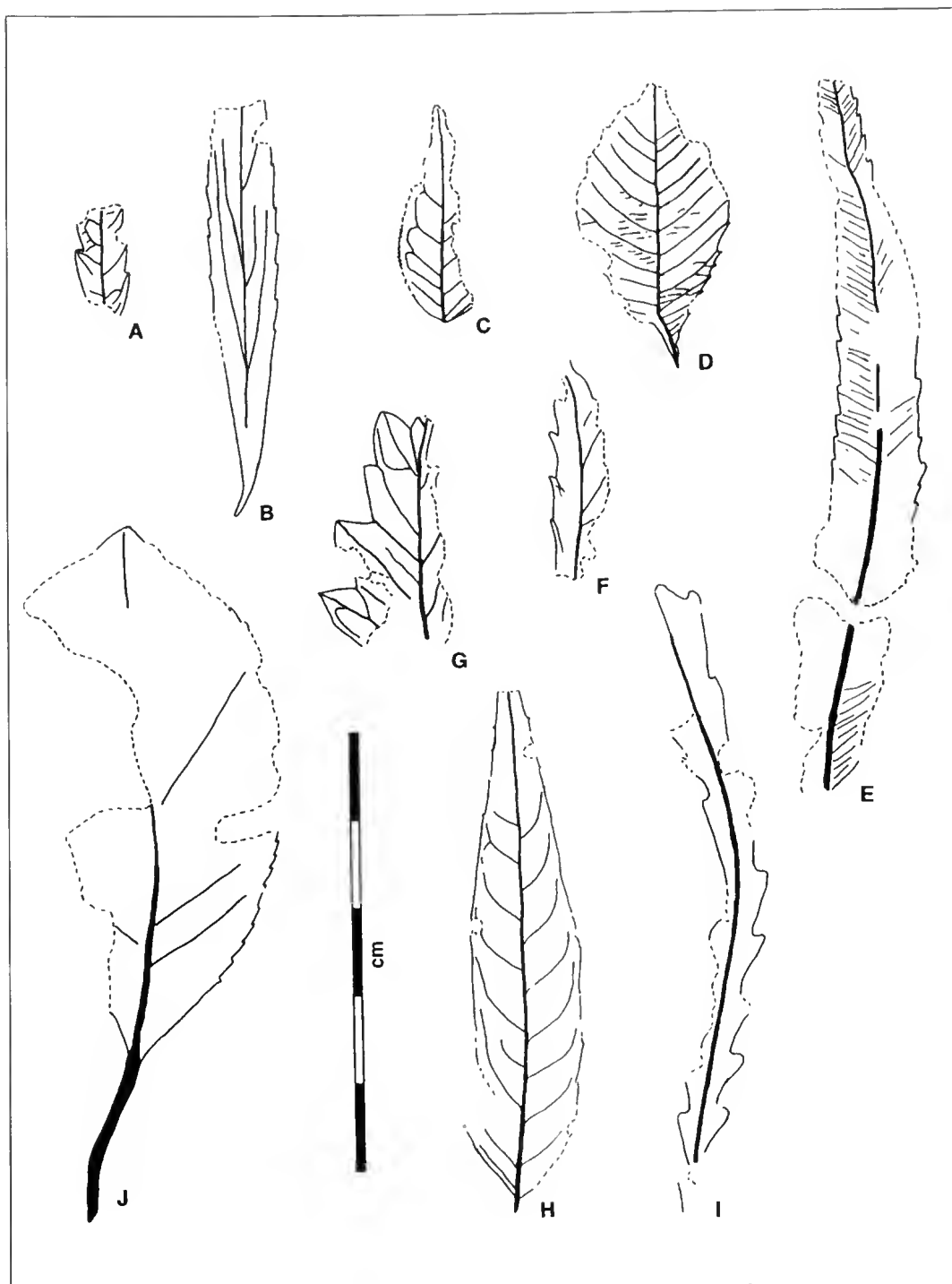


Fig. 16. A, Toothed Margin B, P94103; B, Toothed Margin C, P94197; C, Toothed Margin D, P94185; D, Toothed Margin E, P94147; E, Toothed Margin F, P94299; F, Toothed Margin F, P94254; G, Toothed Margin G, P94128; H, Toothed Margin H, P94253; I, Toothed Margin I, P94213; J, Toothed Margin J, P94320.

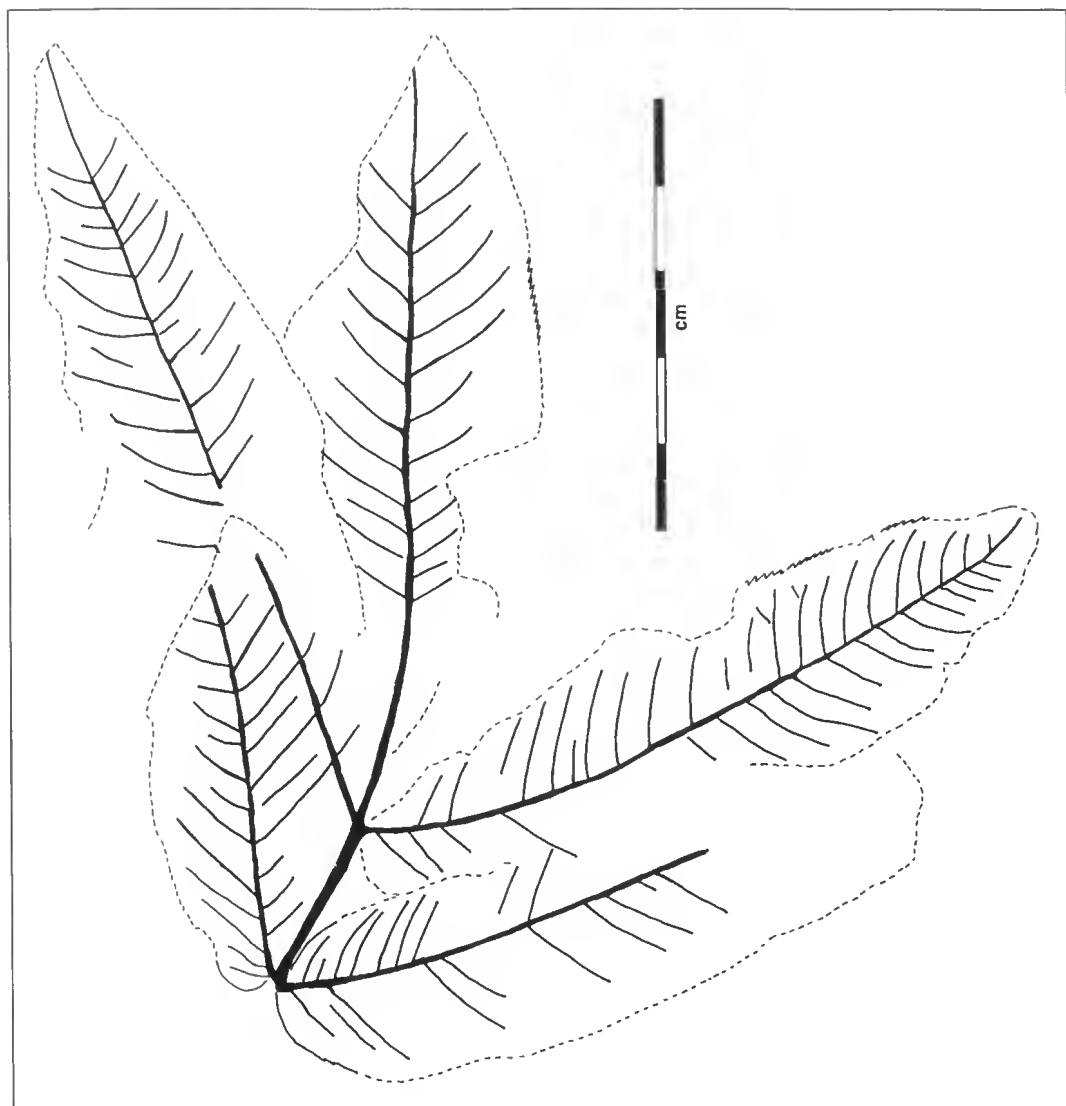


Fig. 17. Compound Leaf A, P94277.

Toothed Margin Type G
(Fig. 16G)

Reference specimen. Locality 1: P94128.

Description. Leaf size: length unknown, preserved length 30 mm, width about 24 mm. Leaf shape: unknown, apex possibly acute, base unknown, petiole unknown. Margin non-entire (toothed), tooth height 2–4 mm, spacing about 7 mm. Venation craspedodromous.

Toothed Margin Type H
(Fig. 16H)

Reference specimen. Locality 2: P94253.

Description. Leaf size: length 65 mm, width 13 mm. Leaf shape: lanceolate, apex attenuate, base obtuse, petiole 1 mm. Margin non-entire (toothed), tooth height about 0.1–0.2 mm, erect, spacing about 1 mm. Venation externodromous.

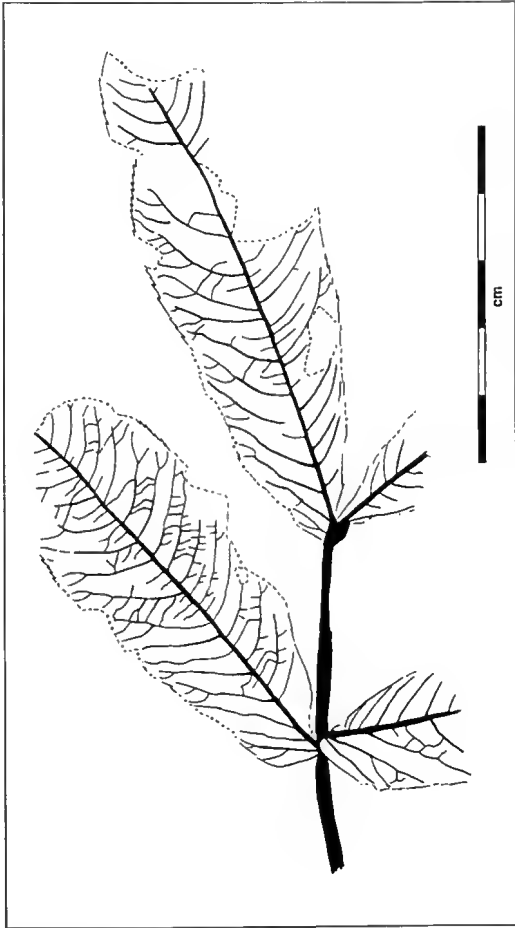


Fig. 18. Compound Leaf A, P94124.

Toothed Margin Type I (Fig. 16I)

Reference specimen. Locality 3: P94213.

Description. Leaf size: length at least 75 mm, width about 8 mm. Leaf shape: lorate, apex unknown, base acute, petiole unknown. Margin non-entire (toothed), tooth height about 1.5 mm, reclined, sinuses rounded, spacing about 5–10 mm. Venation unclear.

Toothed Margin Type J (Fig. 16J)

Reference specimen. Locality 3: P94320.

Description. Leaf size: length 62 mm, width 36 mm. Leaf shape: narrow obovate, apex obtuse (bluntly pointed), base cuneate, petiole 23 mm. Margin non-entire (toothed),

tooth height 0.2 mm, spacing about 2 mm. Venation not preserved.

Compound Leaves (Figs 17–20)

Compound Leaves A, C, D may be Sapindaceae, but no detailed comparisons have been made. Compound Leaf E is trifoliate (Fig. 20A), the leaflets are sessile on the petiole, causing their bases to overlap slightly. The margin is finely toothed. Trifoliate leaves of this general form are common in the Rutaceae, but there are seemingly few with toothed margins as well. *Acradenia franklineae* is an example, but is only toothed on the apical half of the leaflets. A further possibility is with the Cunoniaceae (eg *Pseudoweinmannia lachnocarpa* is grossly similar) but no close comparisons have been made.

Compound Leaf F (Fig. 20B) is represented by a single poorly preserved specimen. The pinnately compound leaf has leaflets which are opposite and the margins appear to be highly sinuous. It is possible this is a fern frond.

Compound Leaf G (Fig. 20C) is represented by a single specimen with a curved, markedly asymmetrical base indicating it is a leaflet from pinnately compound leaf. It shows gross similarity with leaflets in the Simaroubaceae (eg. *Ailanthus integrifolia* B. Hyland) and Meliaceae (eg. *Toona australis* and *Dysoxylum muelleri* B. Gray), but differs in the finely toothed margin. Its identity remains unknown.

Compound Leaf A (Figs 17–18)

Reference specimen. Locality 2: P94277.

Referred material. Locality 1: P94124, P94110 ?P94199. Locality 2: P94273, P94275, P94276, ?P94258. Locality 3: P94280, P94282–P94285, SB969, SB971, SB974–SB976.

Description. Form imparipinnate. Leaf size: estimated length about 110–120 mm, width about 140 mm. Leaflet size: length 55–100 mm, width 12–30 mm.

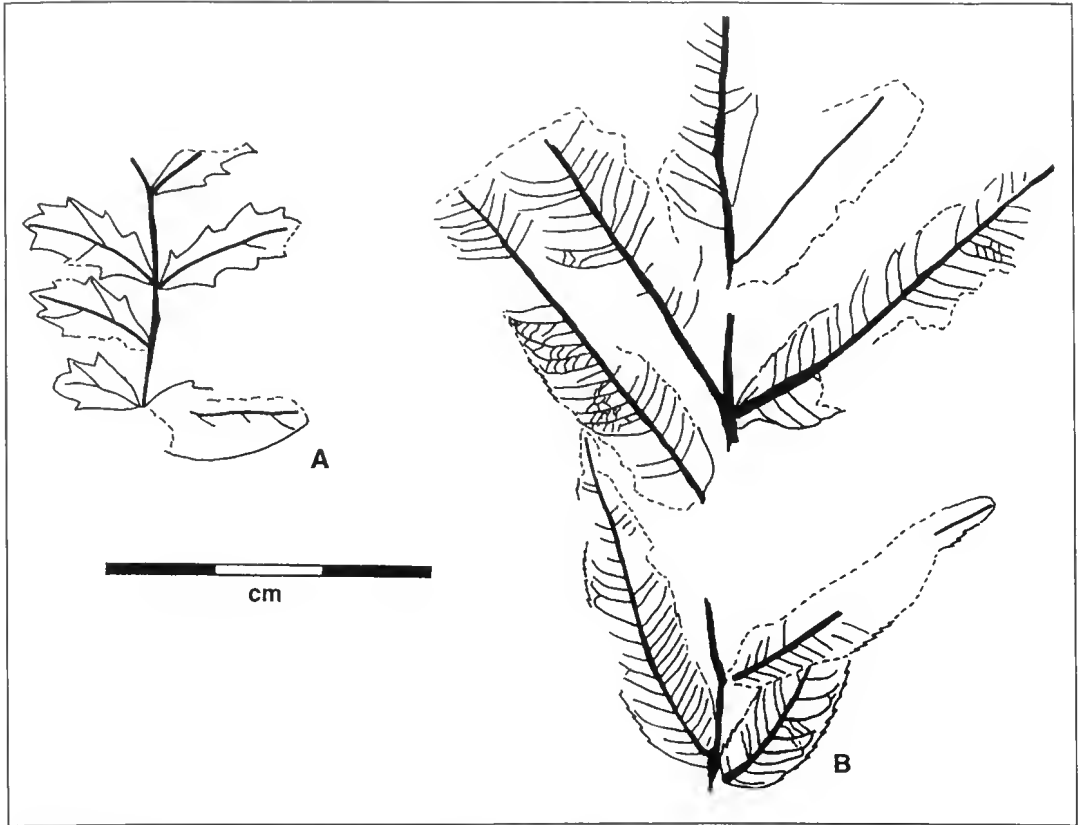


Fig. 19. A, Compound Leaf C, P94281; B, Compound Leaf D, P94326.

Compound Leaf B
(Pole and Bowman 1996)

Leaflet size: length 25-estimated 50 mm,
width 7-15 mm.

Reference specimen. Locality 3: SB950.

Compound Leaf C
(Fig. 19A)

Reference specimen. Locality 3: P94281.

Description. Form pinnate. Leaf size:
preserved length 30 mm, width about 28
mm. Leaflet size: length 9-15 mm, width
about 6 mm.

Compound Leaf D
(Fig. 19B)

Reference specimen. Locality 4: P94326.

Referred material. Locality 1: ?P94109.
Locality 2: ?P94272.

Description. Form imparipinnate. Leaf
size: estimated length 90 mm, width 80 mm.

Compound Leaf E
(Fig. 20A)

Reference specimen. Locality 1: P94100.

Referred material. Locality 1: 94127,
P94146. Locality 3: P94279, P94298.

Description. Form trifoliate. Leaf size:
length 62 mm, width approximately 65 mm.
Leaflet size: length 48-60 mm, width 13-14
mm.

Compound Leaf F
(Fig. 20B)

Reference specimen. Locality 3: P94278.

Description. Form imparipinnate. Leaf
size: preserved length about 80 mm, width
about 50 mm. Leaflet size, length about 30
mm, width about 20 mm.

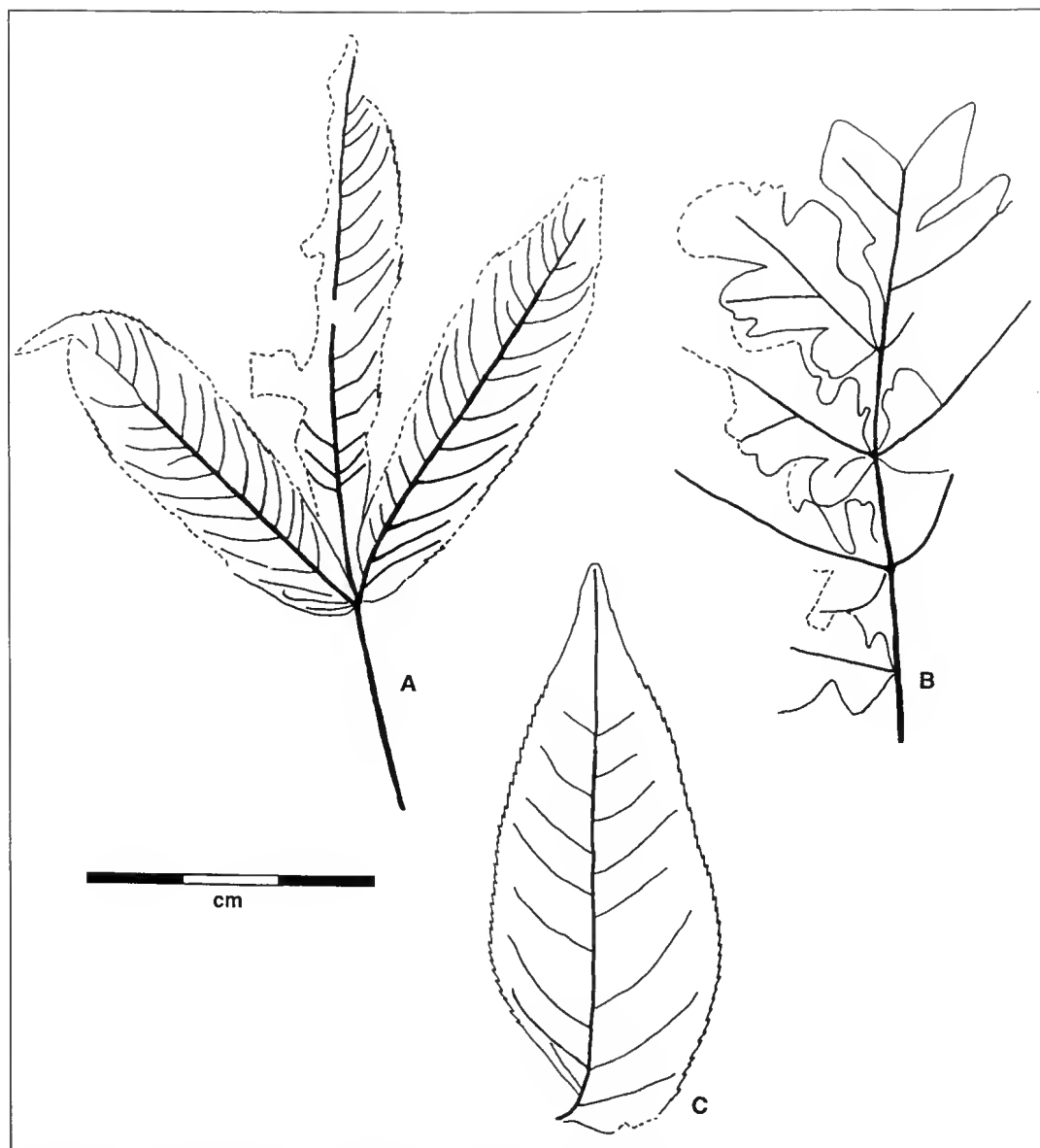


Fig. 20. A, Compound Leaf E, P94100; B, Compound Leaf F, P94278; C, Compound Leaf G, P94126.

Compound Leaf G (Fig. 20C)

Reference specimen. Locality 1: P94126.

Description. Form presumed pinnate.
Leaf size: length and width unknown.
Leaflet size: length 62 mm, width 25 mm.

DISCUSSION

Floristics and modern affinities of the assemblages. *Araucaria* section *Eutacta* is an

important component of the assemblages for estimating the present day affinities of the assemblages. Webb (1959) treats *Araucaria* as a 'special life form' to designate two subformations of Australian forests—mixtures of Vine forest or Vine woodland with emergent *Araucaria*. These were termed Araucarian Notophyll Vine forest (ANVF), and Araucarian Microphyll Vine woodland (AMVW) and occur in mesothermal regions with seasonal drought (Webb 1968). While this is the case today,

extinct species of *Arancaria* in the Australian Tertiary occurred under quite different environmental conditions, namely in forests dominated by Podocarpaceae and *Nothofagus* which were clearly much wetter (Bigwood and Hill 1985; Hill and Bigwood 1987; Hill 1990). These elements are clearly absent from the Melville Island assemblages and support the view that present day vegetation types with *Arancaria* in Australia may be reasonable analogues.

The presence of *Brachychiton* and highly dissected *Grevillea* also support comparison with ANVF and AMVW in the sense that they are characteristic of seasonally dry, more open-canopied vegetation. *Brachychiton bidwillii*, a similar leaf form to the Melville Island fossil, is deciduous and occurs in vine thickets and ecotones of vine thicket or vine forest with eucalypt open forest or woodland (Guymer 1988). The possible representation of Sapindaceae and Rutaceae amongst the compound leaved fossils is also consistent. Young and McDonald (1987) note that these two families are among those that often predominate in Araucarian vine forests. Conversely, they noted that Meliaceae and Proteaceae are two which sometimes disappear altogether or become poorly represented. *Ceratopetalum apetalum* does not normally occur in ANVF or AMVW but may occur close by in a different vegetation type. Its possible occurrence (as Toothed Margin Type A) with *Arancaria* in the Melville Island assemblages suggests a wider range of tolerance than shown by the extant species, or that it is another species.

Close comparison with extant vegetation communities probably cannot be made. Some climate types of the Tertiary probably do not exist today, while there is no doubt many plant associations which contained *Arancaria* have become extinct as a result of the intense anthropogenic burning in the drier parts of Australia. Young and McDonald (1987) note the widespread clearing of Araucarian vine forests in recent time. Some of these communities may have been forests which have owed their composition more to very low nutrient status than low rainfall. As a result of more intense burning and extinction of these communities, the only comparable extant

vegetation may be in areas of low/seasonal rainfall and relatively high nutrients. A false impression of the climate may be gained. P. Latz (pers. comm.) suggested this might be the case for the Melville Island assemblages.

To test this hypothesis, comparison can be made with other fossil assemblages from areas which were relatively dry and had low nutrient levels. Hill and Merrifield (1993) described an Paleogene macroflora from West Dale in Western Australia which was undoubtedly derived from a very low nutrient substrate. The differences from Melville Island are significant. The authors state a 'clear broad-leaved rainforest component' is present. *Nothofagus* is present, and several specimens of Podocarpaceae were collected and identified to two genera, *Retrophyllum* and *Dacrycarpus*. As noted above, these are absent from Melville Island. At least one species of broad-leaved Lauraceae was present. These are generally as common in typical 'rainforest-type' Tertiary assemblages (pers. obs) as they are in rainforest of Australia today. In the Melville Island assemblages there are no leaves which are considered to be potential Lauraceae. *Gymnostoma* was present in Western Australia, but not in Melville Island. Myrtaceae were prominent in the Western Australia species count (8) but were all of generally elliptical form, compared to the single extremely elongate form of Melville Island *Melolencia*. Araucariaceae were present, but as *Agathis*, generally confined to wetter environments today than *Arancaria*.

Of the similarities, at the West Dale locality Proteaceae dominated the specimen and species count (11) and Cunoniaceae (cf. *Callicoma*) was present but highly dissected Proteaceae leaves were not found. Hill and Merrifield (1993) suggested that as the climate dried and possibly became hotter, genera such as *Agathis*, the podocarps, and *Gymnostoma* would have become extinct. There is thus no evidence here to support the idea that the Melville Island assemblages are a result of very low nutrient levels under moderate rainfall, but it is suggested that it could have derived from a Paleogene Western Australian-type flora after rainfall decreased.

Another Tertiary fossil flora which would have grown in very low nutrient conditions is

Nelly Creek, from the south edge of Lake Eyre (Christophel *et al.* 1992). This flora again shows similarities with the Western Australian fossil flora. It has *Agathis*, Podocarpaceae, *Gymnostoma*, and numerous entire-margined, elliptical leaves. Proteaceae and Myrtaceae were prominent. It can again be assumed that rainfall was moderately high, with low nutrient levels, and that some form of rainforest developed. To eliminate these taxa and thus to arrive at a Melville-Island type of assemblage, rainfall presumably decreased.

Nearby the Nelly Creek fossils are deposits of 'silcrete floras'. These are fossil leaves in silica-cemented sandstone (silcrete), which are widely distributed across South Australia. Their age is unclear, but in some instances appear to be Eocene. Greenwood *et al.* (1990) reported *Brachychiton*, narrow, sometimes falcate Myrtaceae leaves, as well as toothed leaves possibly similar to the 'Toothed A' leaves described here. Christophel *et al.* (1992) also noted a narrow, linear, entire-margined Proteaceae leaf occurred in the silcrete. I suspect that the silcrete floras may be one of the major keys, not only to the floristic identity of some Melville Island fossils, but also to their age.

Assemblages. The number of individual specimens in the main assemblages is indicated in Table 1. Locality 4 has not been shown as it is essentially just ?fern fronds with a very few angiosperm leaves. Within Locality 1, specimens have been divided as coming from the purple mud facies, or otherwise. The purple mud facies has a distinct assemblage dominated by *Smilax* (this is the only assemblage containing *Smilax*), and 'Toothed A' subdominant. Compound leaves and *cf. Dilobeia* /*Liriodendrites* are absent from the purple mud facies.

The sediments from Locality 1 which are not purple mud, are heterogeneous, but sandier or siltier, and are more similar to lithologies from Localities 2 and 3. The assemblages from these other lithologies are also similar, with *Smilax* absent, and compound leaves, *cf. Dilobeia* /*Liriodendrites* and *Grevillea* important. The taxonomic

differences may reflect the different substrates, the purple mud supporting a community requiring higher-nutrient levels than the community occupying sandier substrates.

There is no suggestion that the floristic differences between the lenses were due to anything other than normal spatial heterogeneity or from relatively short-term (i.e. a few hundred years) variations in floristic composition.

Foliar physiognomy. The leaf assemblages have a remarkably distinct physiognomic 'signature'. The assumption is followed here that the physiognomic signature reflects, in some way, the climate in which the original plant communities lived in. Physiognomy of individual leaves is shown numerically in Table 2, and of taxa in Table 3.

The length of leaves was measured, or mostly estimated, in all cases where the leaf was considered complete enough to allow it. Leaflets of compound leaves were treated as individual leaves, but all the deeply divided *Grevillea* leaves were ignored. Their inclusion would probably require measuring the lengths of each lobe, and the statistical value of attempting this on the few leaves is dubious. The over-all average leaf length of 64 mm indicates that the leaf area falls within the microphyll category (Webb (1959) gave the boundary between microphyll and notophyll leaves as 76 mm for leaves of lanceolate or elliptical shape). This is relatively small - Webb (1959) documented that Australian tropical and subtropical forests, where conditions were optimal, had significant proportions of notophyll, and even mesophyll leaves, whereas microphyll leaves became more important as temperatures cooled, or rainfall became limiting. Likewise, Specht and Womersley (1979) noted that in Borneo, under presumably optimal rainfall and temperature, Dipterocarp forests had an average leaf size of mesophyll, whereas the 'kerangas', on nutrient poor soils, had an average leaf size of notophyll. The small leaf size of the Melville Island leaves could be a reflection of low nutrient levels of their substrate. The leaves of the purple mud

Table 1. Specimen counts for each assemblage. Locality 4 is omitted as it contains mainly the ?fern type and one Compound Type D leaf.

	Total	Locality 1 purple mud facies	Locality 1 not purple mud	Locality 2	Locality 3
<i>Araucariaceae</i>	12	9			3
<i>Cupressaceae</i>	4	1	3	1	3
<i>Brachychiton</i>	2	1	1		
<i>cf. Dilobeia</i>	20		4	1	12
<i>Grevillea cf. whitiana</i>	30	5	11	4	10
<i>G. cf. longifolia</i>					1
<i>G. cf. dryophylla</i>					1
?Legume	1	1			
<i>Melaleuca</i>	12	9	4		1
<i>Smilax</i>	38	38			
Entire A	20	4	3	2	9
Entire B	2	3	1	1	
Entire C	1		1		
Entire D	1		1		
Entire E	1	1			
Entire F	5	3	2		
Toothed A	44	24	14	3	2
Toothed B	3		1	1	1
Toothed C	1	2			
Toothed D	2	1			1
Toothed E	4		1		1
Toothed F	1				1
Toothed J	1				1
Toothed G	1				
Toothed H	1				
Toothed I	1				1
Compound A	14		1	4	9
Compound B	1				1
Compound C	2		1		1
Compound D	3		2		
Compound E	4		1		2
Compound F	1				1
Compound G	1		1		
Unallocated	18	4	4	7	4

facies, which might be expected to have a higher nutrient level than the sandier substrates, are larger. They have an average length of 75 mm which however, is still within the microphyll category. Leaf length of the fossils suggests temperature and/or rainfall was suboptimal.

It has long been observed that tropical rainforest is overwhelmingly dominated by leaves which have entire margins. Richards

(1952) provided outline drawings of tropical rainforest leaves to emphasise this, as well as their overall similarity of shape - mostly oblong-lanceolate to elliptical. When it comes to estimating the proportion of entire margined leaves in the Melville Island assemblages, a difficulty arises, which, in itself, suggests something was unusual about the environment. In short, the typical tropical rainforest shape of leaf is rare. Whereas *cf.*

Table 2. Physiognomic summary based on individual leaves and leaflets.

	Overall total	Locality 1	Locality 2	Locality 3	Locality 1 purple mud	Locality 1 not purple mud	Overall total except purple mud
Angiosperm leaves	297	163	35	90	96	68	201
Average length	64mm	71mm	87mm	52mm	75mm	60mm	59mm
Entire (no lobes)	27%	41%	9%	11%	56%	16%	14%
Entire (no lobe/linear)	15%	27%	3%	Nil	43%	9%	2%
Toothed	49%	42%	66%	52%	28%	59%	58%
Lobed	18%	13%	14%	24%	6%	24%	23%
Compound leaflets	27%	14%	46%	39%	Nil	34%	40%

Table 3. Physiognomic summary based on taxa.

Angiosperm taxa with leaves	30%
Entire (no lobes)	27%
Entire (no lobes, not linear)	17%
Toothed	57%
Lobed	10%
Compound	23%

Dilobeia/Liriodendrites has an entire margin, it is deeply bi-lobed, the *Grevilleas* do not have teeth, but are deeply lobed/dissected. The 'Entire Margin A' and the *Melaleuca* leaves are entire, but are extremely elongate. Excluding the lobed, or lobed and elongate leaves, entire margined proportions are extraordinarily low: overall between 11% and 19% of the taxa, or 15% and 30% of individuals.

The purple mud of Locality 1, dominated by the entire-margined *Smilax*, still has only between 40% and 60% of individuals with entire margins. However, the real amounts of *Smilax* and 'Toothed Leaf B' in the purple mud, and their proportions to the rarer taxa, will be higher than the number actually catalogued, because of many over-lapping and fragmentary specimens, and the need to choose which individuals to expose completely. If the amounts of these two taxa were up to ten times more than those catalogued, a probable over-estimate, the entire-margined proportion would rise to a little over 60%.

Excluding *Smilax*, entire margined leaves which are unlobed or not elongate, are

virtually absent. Normally (e.g. Bailey and Sinnott 1916; Wolfe 1979) entire margined leaves are contrasted with toothed leaves, and low figures for entire margins are taken as indicating cool conditions. This cannot be done directly for these assemblages because of the lobed leaves which are not included in either category. Toothed margin percentages were calculated separately based on the 'Toothed' taxa and the 'Compound' leaves, all of which are toothed. Over all, toothed leaves are about double, or more, than entire margins, on taxon or individual counts. Only in the purple mud facies do these figures reverse. The over-all figures suggest relative coolness. The figures from the purple mud might be explained by the overwhelming dominance of *Smilax*, a climber and not a canopy tree, unduly skewing what would be a dominance by toothed types. The number of leaflets from compound leaves in the assemblages, is striking. Overall the figure is 27%, but they are notably absent from the purple mud. Omitting this assemblage, they form 58% of all individuals, and 23% of all taxa. Even this is probably an underestimate, as it is based on taxa which are clearly compound - other forms, like Toothed D and Toothed I may also be leaflets.

Such a high proportion of compound leaflets is unusual in a fossil assemblage - in most cases it might be expected that the leaves disaggregated into their leaflets during taphonomic processes. The figure may also be giving some form of physiognomic signal on the environment. For instance, Bews (1925, 1927) found in

southern Africa that the percentage of tree species with compound leaves was greater in areas with seasonal drought than well-watered regions. Webb (1959) found the highest percentage of individuals with compound leaves in Australian forests (c. 60%) was in Araucarian Microphyll Vine woodland. This is significant given the presence of *Araucaria* throughout the assemblages. Givnish (1978) reasoned that compound leaves were 'adaptive in at least two sorts of environmental contexts: in warm seasonally arid situations that favour the deciduous habit, and in light gap and early successional vegetation where rapid upward growth and competition for light favour the cheap throwaway branch'. The later context is unlikely to be the controlling factor here. The purple mud assemblage, dominated by *Smilax*, is the most likely to be sampling such an environment, but compound leaves are absent from it.

Pronounced lobing is present on three taxa: cf. *Dilobeia/Liriodendrites*, *Brachychiton*, and *Grevillea*. Overall, and in most assemblages it is close to 20% (10% of all taxa), except in the purple mud, where it is 6% and probably reflects the absence of cf. *Dilobeia/Liriodendrites*. Wolfe (1993) concluded that lobing is most characteristic of microthermal environments and was common in open-canopy vegetation. In Australia, as noted above, these forms of *Brachychiton* and *Grevillea*, and *Banlinea*, as a possible physiognomic analogue of cf. *Dilobeia/Liriodendrites*, are characteristic of warm and seasonally dry vegetation.

It is important to understand that evidence of rainfall seasonality in Australia's far north during the Paleogene (see below for age) does not contradict the hypothesis of the tracking latitude of Sub Tropical High Pressure (STHP) cells overtaking Australia from the south in the Miocene (Bowler 1982; Pole 1993). The limits of the migrating STHP hypothesis are likely to be in the Oligocene when Australia's continued northward movement caused the formation of the circumpolar ocean current (Kennett 1977). Before this, boundary conditions were completely different—the zonal atmospheric system as we know it may not have existed.

In summary, the physiognomy confirms the conclusions of Pole and Bowman (1996), that the climate was 'warm, but not tropical, and rainfall was probably seasonal'.

Reassessment of the age. The Van Diemen Sandstone is still not precisely dated. No carbonaceous lithologies were encountered on this expedition, so palynology is unlikely to be of direct use, though has not been ruled out. No marine fossils were found either. However, two lines of reasoning suggest the formation may be of Paleogene age, rather than Neogene.

Firstly, the sediments appear to have been deposited by a constantly flowing stream, rather than one of intermittent or ephemeral nature. From a variety of palynological evidence, Australia was progressively drying out during the later Tertiary, and streams were likely to have become more seasonal. Megirian (1992) interpreted the Miocene Carl Creek Limestone of Riversleigh, northwestern Queensland, as accumulating under relatively dry, perhaps semi-arid conditions. This is consistent with the palynological evidence. Other Miocene limestones across northern Australia indicate these conditions were widespread at the time and do not suggest a stable catchment supply for large, stable rivers.

Secondly, the climate suggested by the leaf physiognomy - warm, but not tropical - would be more consistent with an older age, when Australia was situated at more southern latitudes. Feary *et al.* (1991) inferred subtropical conditions for northernmost northeast Australia throughout the Paleogene based on carbonate sedimentation, with tropical conditions not being realised until the Early Miocene. Earlier inferences of tropical conditions for this region in the Paleogene by Davies *et al.* (1989) are apparently incorrect. In addition, Thunell *et al.* (1994) have provided evidence that even during the height of the last glaciation, temperatures in the tropical Western Pacific remained much as they are today. This suggests that land temperatures at tropical latitudes in Australia have also remained much the same throughout the Tertiary, and that the greatest fluctuations have been polewards.

In addition, work in progress on the Paleogene fossil flora of Redbank Plains,

near Brisbane, has shown deeply dissected Proteaceae leaves like *Grevillea* sp. cf. *G. whitiana* are a feature. Perhaps these kind of Proteaceae were a dominant feature of Paleogene vegetation in northern Australia. They do not appear to have been common in southern fossil floras.

Future work. It is clear from the brief exploration that more fossil localities exist on Melville Island, and may be widespread. Future collecting would extend the taxonomic database, and there is much scope for a detailed sedimentological analysis.

A much better understanding of the climate will result from sampling present day plant communities with transects from those growing on poor substrates to those on more nutrient rich ones. The lowlands of Borneo will make an excellent study area for this approach.

A more precise date for the fossils is now of utmost priority. One approach would be to try and trace the Van Diemen Sandstone offshore in drill cores, where microfossils may still be preserved. Finding floristic matches with specimens in other, better dated fossil assemblages in northern Australia, is another.

SUMMARY

The fossil flora of Melville Island is an extremely important addition to the paleobotanical and paleoclimatic knowledge of Australia. It is so far the best known Tertiary site with plant macrofossils from the northern 50% of Australia and thus provides an important control point for developing biogeographic theories. Although deep weathering has destroyed much valuable detail, enough remains to be useful. The genera which have been identified can be related to the present vegetation of Australia, and point towards drier, more seasonal forests. The foliar physiognomy is distinct and tells a similar story. The age of the deposit is still uncertain, but the evidence is pointing towards the Paleogene, perhaps Paleocene or Eocene. The evidence of seasonal climate so early in the Tertiary of Australia is the most important conclusion of this work.

ACKNOWLEDGMENTS

There are many people to thank whose efforts resulted in this report. David Bowman initially pushed the idea, Bill Panton liaised with the Tiwi Land Council, and Ian Cowie did much of the logistical organisation. Nigel Scullion with his boat *Kalidris* and crewman Sean Smith, took care of most of the transportation and catering. Dirk Megirian of the Museum and Art Gallery of the Northern Territory participated in the expedition, supplied equipment, and provided working space at the museum for packaging. The other participants, in no particular order, who also sweated it out in harsh conditions, braved the crocodile-infested waters, stolidly watched as I had to leave some of their efforts on the beach, and, above all, provided useful discussion and terrific camaraderie, are Peter Latz, David Albrecht, Paul Munns, Greg Leach. I thank Bob Hill, Department of Plant Science, University of Tasmania, for supplying me with workspace and logistical support, and Clyde Dunlop of the Northern Territory Herbarium for his support and help. The final corrections were made at the Department of Botany, University of Queensland, with funding via ARC grant to M.E. Dettmann and G. Stewart. The comments of two anonymous referees helped the manuscript. Finally, I am extremely grateful to the Parks and Wildlife Commission of the Northern Territory for providing the majority of the funds for this project.

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Accepted 28 October, 1997

FURTHER STUDY ON AUSTRALIAN HETEROMYSIDS (CRUSTACEA: MYSIDACEA)

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ABSTRACT

Three new species of heteromysids are described. A new species, *Heteromysis (Olivaemysis) maxima*, collected from South Australia, is distinguished from allied species by a combination of characters in the shape of the rostrum, the spination on the carpopropodus of the thoracic endopod 3, and the numbers of spines on the uropodal endopod and the telson. The second species, *Heteromysoides nana* sp. nov., from the Northern Territory, is identified by the telson without apical cleft, the uropodal endopod without spines on the inner margin and the eyestalk with rounded anteromedial corner. The last species, *Heteromysoides sahulensis* sp. nov., captured from the Sahul Shelf, is different from other species of the genus in the shapes and armatures of the uropod and the telson.

KEYWORDS: Crustacea, Mysidacea, *Heteromysis*, *Heteromysoides*, new species, Australia

INTRODUCTION

Heteromysids stored in the Northern Territory Museum, Darwin, were previously reported by the present author (Murano 1988). A further two new species were found among the mysid specimens which were again sent me for identification from the Northern Territory Museum. A third new species also described here was found among mysid material collected from the Sahul Shelf during a cruise of RV *Hakuho Maru* of the University of Tokyo. In this paper descriptions of the three new species are given. The type specimens are stored in the Museum and Art Gallery of the Northern Territory (NTM), Darwin, Australia.

SYSTEMATICS

Heteromysis (Olivaemysis) maxima sp. nov. (Figs 1-3)

Type material. HOLOTYPE – adult male, NTM Cr. 006872, 8.6 mm, Edithburgh Jetty, South Australia, 34°55'S, 137°45'E, 8 m, inside sponge on jetty pylon, 29 December 1989.

Description. Carapace produced anteriorly into triangular rostrum with

broadly rounded apex extending beyond basal margin of antennular peduncle, lateral margins of rostrum nearly straight (Fig. 1A); anterolateral corners of carapace rounded; posterior margin emarginate, leaving last thoracic somite exposed dorsally.

Eye extending slightly beyond distal end of antennular peduncle segment 1, longer than wide, with hemispherical cornea narrower than stalk and occupying less than half of whole organ; eyestalk with small but prominent triangular denticle at distal end of medial margin (Fig. 1A).

Antennular peduncle robust, segment 1 with prolonged distolateral angle tipped with several setae; segment 2 with long medial margin and very short outer margin for oblique connection with segment 3, armed on medial margin with one flagellate, flattened spine and one ordinary seta; segment 3 armed on middle of medial margin with one seta and at distomedial corner with one flagellate spine and three setae, one of which is stout and directed outwardly (Fig. 1A).

Antennal scale shorter than antennular peduncle, elongated elliptical, 2.5 times longer than broad, setose all round, inner margin more convex than outer, distal suture invisible (Fig. 1B). Antennal peduncle

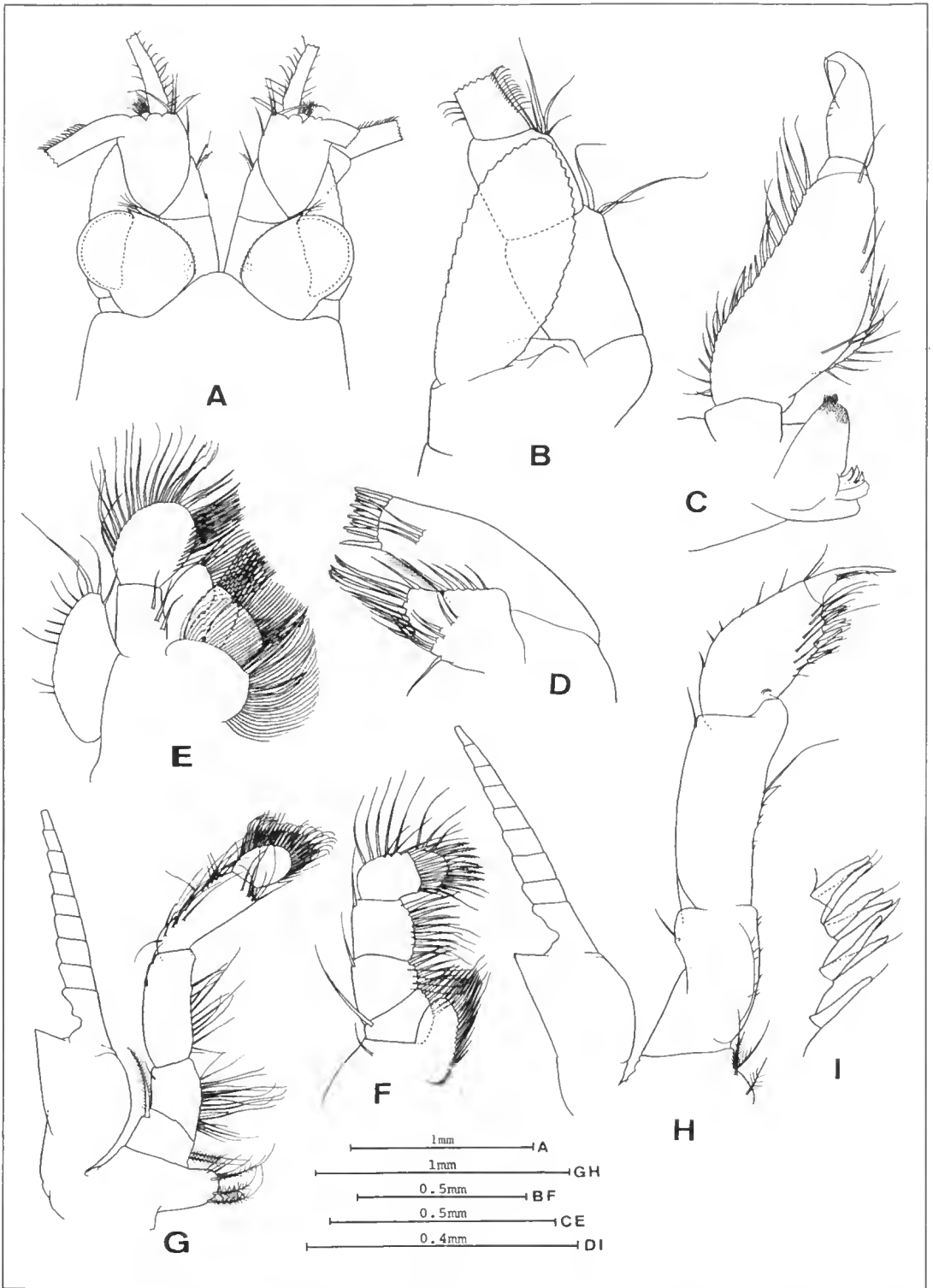


Fig. 1. *Heteromysis (Olivaemysis) maxima* sp. nov., holotype. A. anterior end of body; B. antenna; C. mandible; D. maxillule; E. maxilla; F. endopod of first thoracic limb; G. second thoracic limb; H. third thoracic limb; I. spination on inner margin of carpopropodus of third thoracic endopod.

extending slightly beyond antennal scale, segment 2 longest (Fig. 1B).

Mouth parts and thoracic endopods 1 and 2 as shown in Fig. 1C–G.

Thoracic endopod 3 robust, merus 2.5 times longer than broad, with one long seta and about eight short setae at middle of inner margin and one seta near distal end of outer margin; carpopropodus less than twice as long as broad, becoming narrower distally, with one single and three paired spines (seven spines in total) on distal half of inner margin, these spines armed with a single subterminal seta; terminal claw very stout (Fig. 1H–I). Carpopropodus of thoracic endopods 4, 5 and 7 divided into four, nine and three subsegments, respectively; dactylus small, terminating in slender claw (Fig. 2A–C). Condition in endopods 6 and 8 unknown due to loss. Thoracic exopods distal to basal plate 9-segmented, basal plate with pointed distolateral corner (Fig. 1G–H; Fig. 2A–B). Penis cylindrical, slightly curved anteriorly, with bilobed apex, outer margin with short seta at proximal third (Fig. 2D–F).

Abdominal somites 1–5 subequal, somite 6 slightly longer than others. Pleopods uniramous, unsegmented, increasing in length from first to fifth pair; pleopods 3 and 4 modified, armed on inner margin of distal ramus with eight spines tipped with short seta; pleopod 5 with one long and three short setae on apex, latter three setae directed distally, inwardly and outwardly, respectively (Fig. 3A–E).

Uropod with both rami broad, setose all round; endopod reaching tip of longer apical spine on telson, with four to five spines in statocyst region on inner margin; exopod overreaching endopod for 1/7 of its length (Fig. 3F–G).

Telson longer than abdominal somite 6, triangular with apical sinus, 1.3 times as long as maximum breadth at base; lateral margin slightly concave in proximal half and slightly convex in distal half, furnished throughout entire length with 24–25 spines, posterior spines becoming progressively longer and more sparse distally; each apex of lobes with two spines, inner spine shorter than distalmost spine on lateral margin, outer

spine more than twice as long as inner, longest among marginal spines of telson; apical sinus diverging, about 1/4 of telson length, with about 35 spinules along entire length of margin.

Remarks. The genus *Heteromysis* comprises as many as 51 species (Müller 1993). Among them, this new species resembles *H. ageles* Modlin, 1987a, *H. bredini* Brattegard, 1970, *H. (Olivaemysis) sexspinosa* Murano, 1988, and *H. tuberculospina* Modlin, 1987b, in: (1) the cyc is provided with a denticle at the distomedial angle of the stalk, (2) the thoracic endopod 3 has a moderately developed carpopropodus, (3) the male pleopods 3 and 4 become narrower distally and are armed with a row of flagellate spines on the inner margin, and (4) the telson is armed with spines throughout the margin.

Heteromysis maxima sp. nov., however, differs from the latter four species as follows: (1) the rostrum is triangular with broadly rounded apex in the new species while narrowly rounded or obtusely pointed in the latter four species, (2) the spines on the carpopropodus of the thoracic endopod 3 are present on the distal half in the new species but almost the entire length in *H. tuberculospina*, (3) the endopod of uropod is armed with four or five spines in the new species compared with two in *H. sexspinosa* and *H. ageles*, (4) the number of the lateral spines of the telson is greater in the new species than in the latter four species: 24–25 in the new species compared with 14–15 in *H. ageles*, 19–20 in *H. bredini*, 18–19 in *H. sexspinosa* and 17–18 in *H. tuberculospina*, (5) the distal sinus of the telson in the new species is fringed with more spines than in the latter four species: 35 in the new species compared with 12 in *H. ageles*, 31 in *H. bredini*, 25 in *H. sexspinosa* and 18–20 in *H. tuberculospina*, (6) the new species is considerably larger in body size than the latter four species: 8.6 mm in the new species as against 4.0–5.5 in *H. ageles*, 5.8 mm in *H. bredini*, 5.9 mm in *H. sexspinosa* and 2.7–4.8 mm in *H. tuberculospina*.

Etymology. The species name *maxima* refers to large body size.

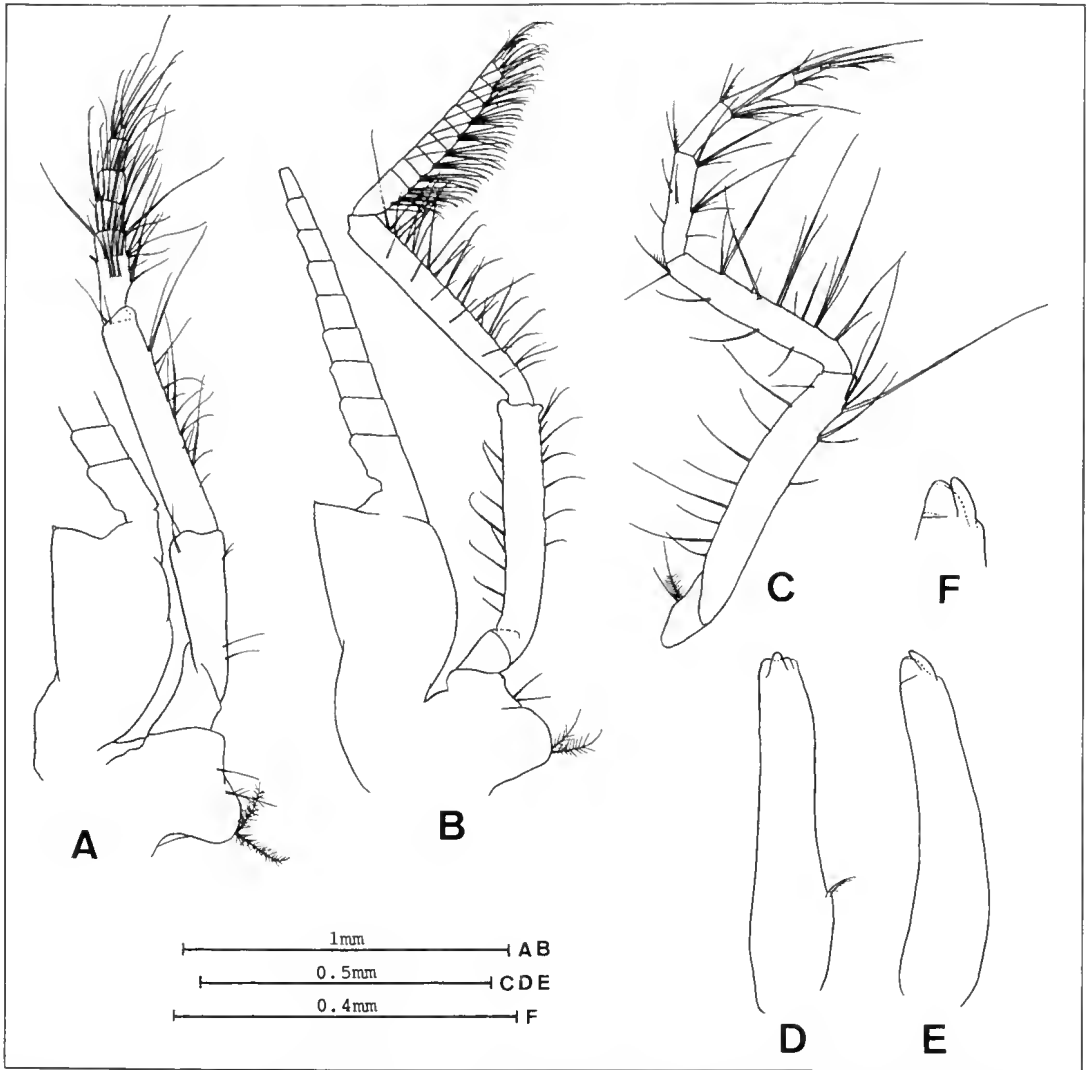


Fig. 2. *Heteromysis (Olivaemysis) maxima* sp. nov., holotype. A, endopod of fourth thoracic limb; B, fifth thoracic limb; C, endopod of seventh thoracic limb; D, penis, posterior view; E, penis, lateral view; F, extremity of penis.

***Heteromysoides nana* sp. nov.**
(Figs 4, 5)

Type specimen. HOLOTYPE – adult female with embryos, NTM Cr. 008032, 3.3 mm, Channel Island, Northern Territory, mud around mangroves, 2 July 1991, coll. K. Coombes.

Description. Body depressed dorsoventrally. Frontal margin of carapace broadly rounded, not produced anteriorly, covering basal part of eyestalks (Fig. 4A); anterolateral corner of carapace rounded; posterior margin emarginate, leaving last thoracic somite exposed dorsally.

Eye large, subquadrate, flattened, covering major part of antennular peduncle segment 1 in dorsal view; eyestalk with rounded anteromedial corner, medial margins overlapping each other; cornea occupying distolateral corner of stalk, with weakly angulate corner (Fig. 4A).

Antennular peduncle: segment 1 with prolonged distolateral corner armed with several setae; segment 2 short, triangular, with long seta on distomedial corner; segment 3 longer than segment 1, broader than segment 2, with one long seta on middle of medial margin and four setae at distomedial corner (Fig. 4A).

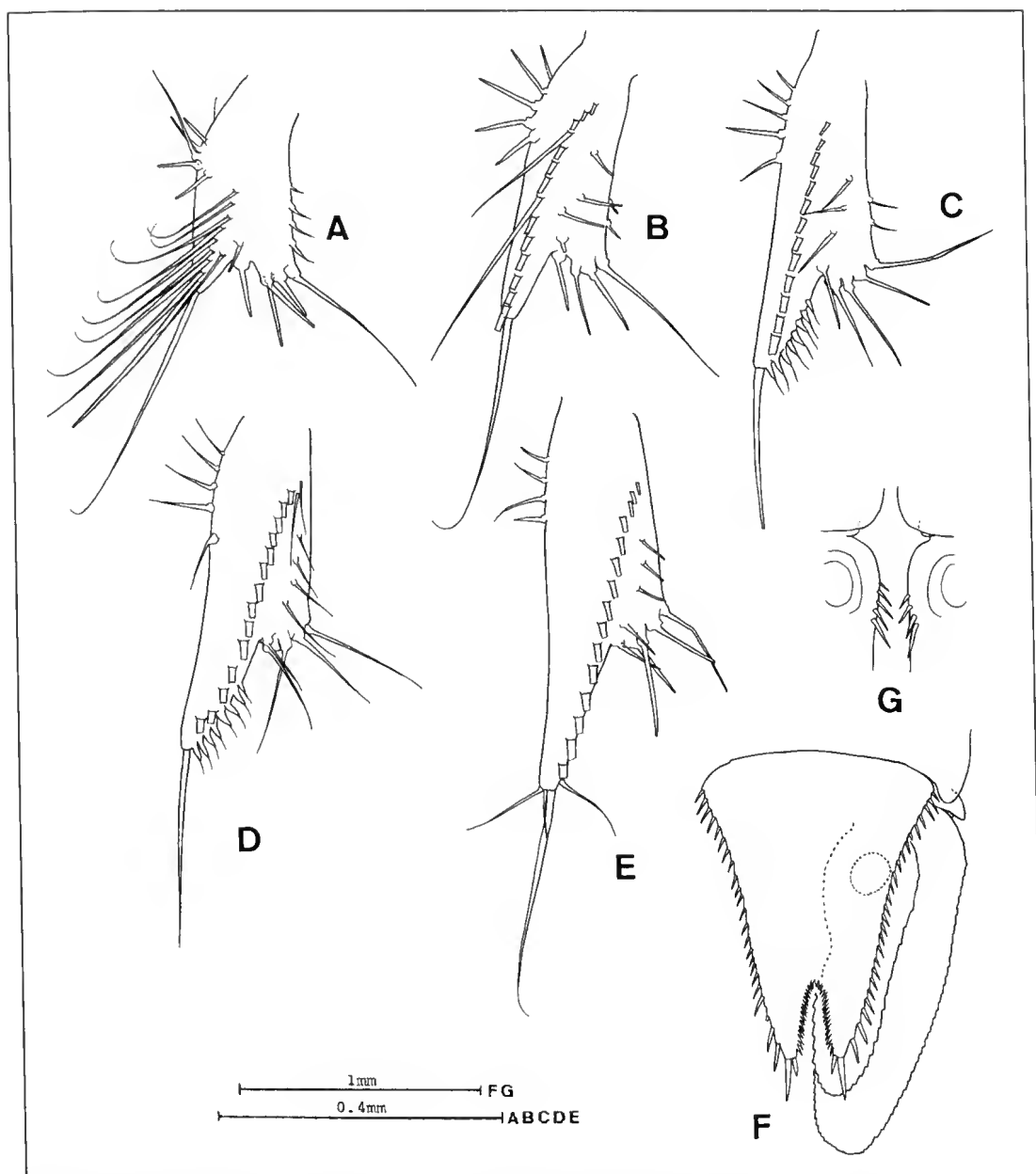


Fig. 3. *Heteromysis (Olivaemysis) maxima* sp. nov., holotype. A, first pleopod; B, second pleopod; C, third pleopod; D, fourth pleopod; E, fifth pleopod; F, uropod and telson; G, proximal part of uropod, ventral view.

Antennal peduncle as long as antennular peduncle, segment 2 twice as long as broad, longer than either of segments 1 and 3; sympod with distolateral corner produced into acute tooth (Fig. 4B). Antennal scale elongated elliptical, setose all round, nearly three times longer than maximum breadth, not extending to distal end of antennal peduncle, medial margin more convex than

lateral margin, distal suture marked off at distal 1/11 (Fig. 4B).

Labrum wider than long, with frontal margin rounded. Mandibular palp (Fig. 4C): segment 2 with three long setae on distal margin, two short setae on outer margin and 1 short seta on inner margin; segment 3 short, outer margin with row of close-set marginal setae, medial margin rounded.

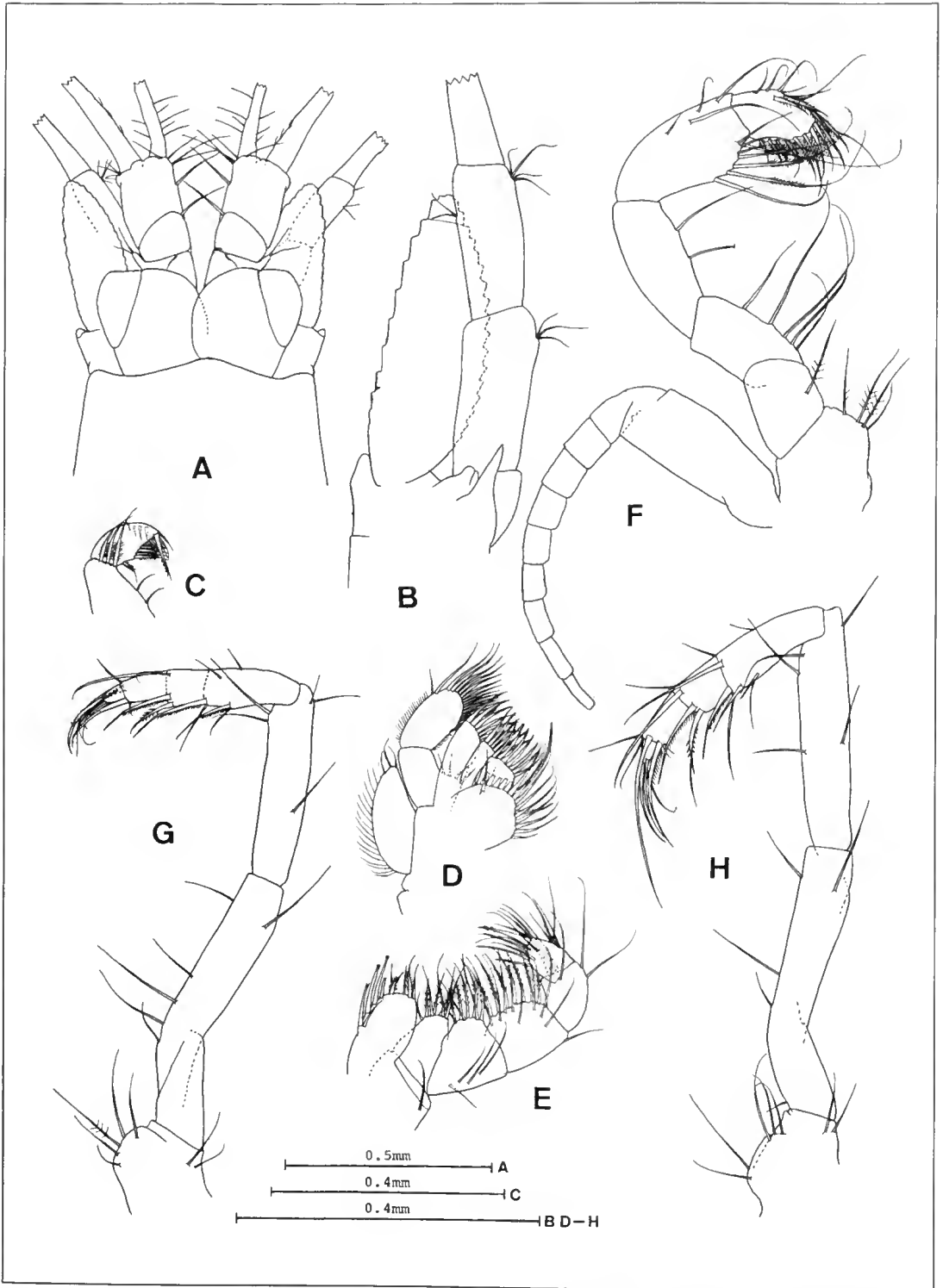


Fig. 4. *Heteromysoides nana* sp. nov., holotype. A, anterior end of body; B, antenna; C, distal part of mandibular palp; D, maxilla; E, endopod of first thoracic limb; F, second thoracic limb; G, endopod of third thoracic limb; H, endopod of fourth thoracic limb.

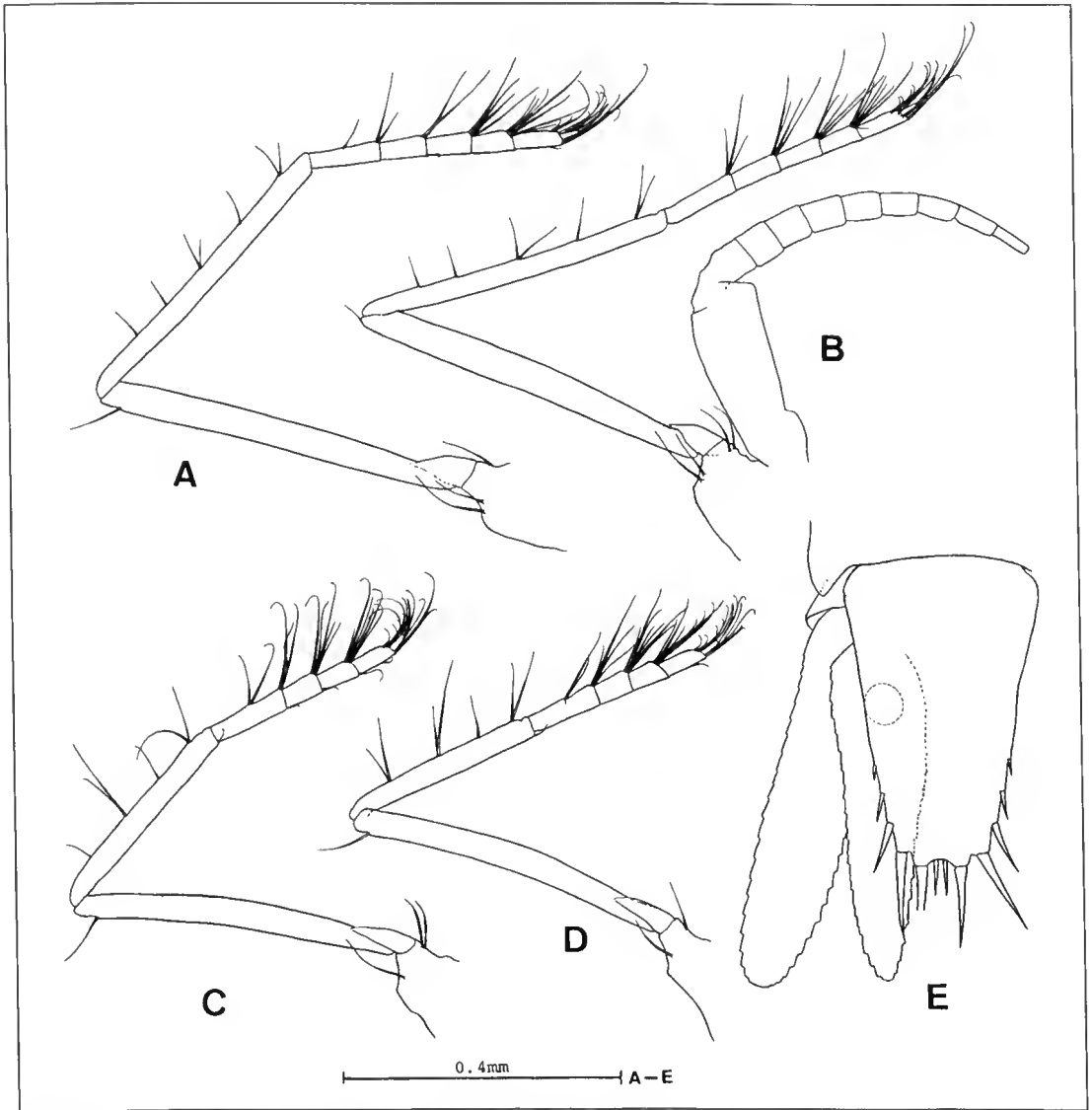


Fig. 5. *Heteromysoides nana* sp. nov., holotype. A, endopod of fifth thoracic limb; B, sixth thoracic limb; C, endopod of seventh thoracic limb; D, eighth thoracic limb; E, uropod and telson.

Maxilla (Fig. 4D): endopod with distal segment longer than proximal segment, heavily setose, endites well developed, densely setose; exopod small, not reaching distal margin of proximal segment of endopod, with feeble marginal setae except for three stout apical setae (Fig. 4D).

Thoracic endopod 1: endite of basis well developed, larger than ischium, with three or four forked setae (one seta broken off) on medial margin, medial margins of ischium, merus and carpus heavily setose; dactylus

with stout terminal claw (Fig. 4E). Thoracic endopod 2 built stoutly; ischium less than twice as long as broad, with five long setae on inner margin, merus more than twice as long as broad, with two setae on inner margin, carpopropodus twice longer than broad; with eight long setae on distal half of inner margin; dactylus with many marginal plumose setae and long naked setae (Fig. 4F). Thoracic endopod 3 rather slender, merus 4.5 times longer than broad; carpopropodus imperfectly divided into

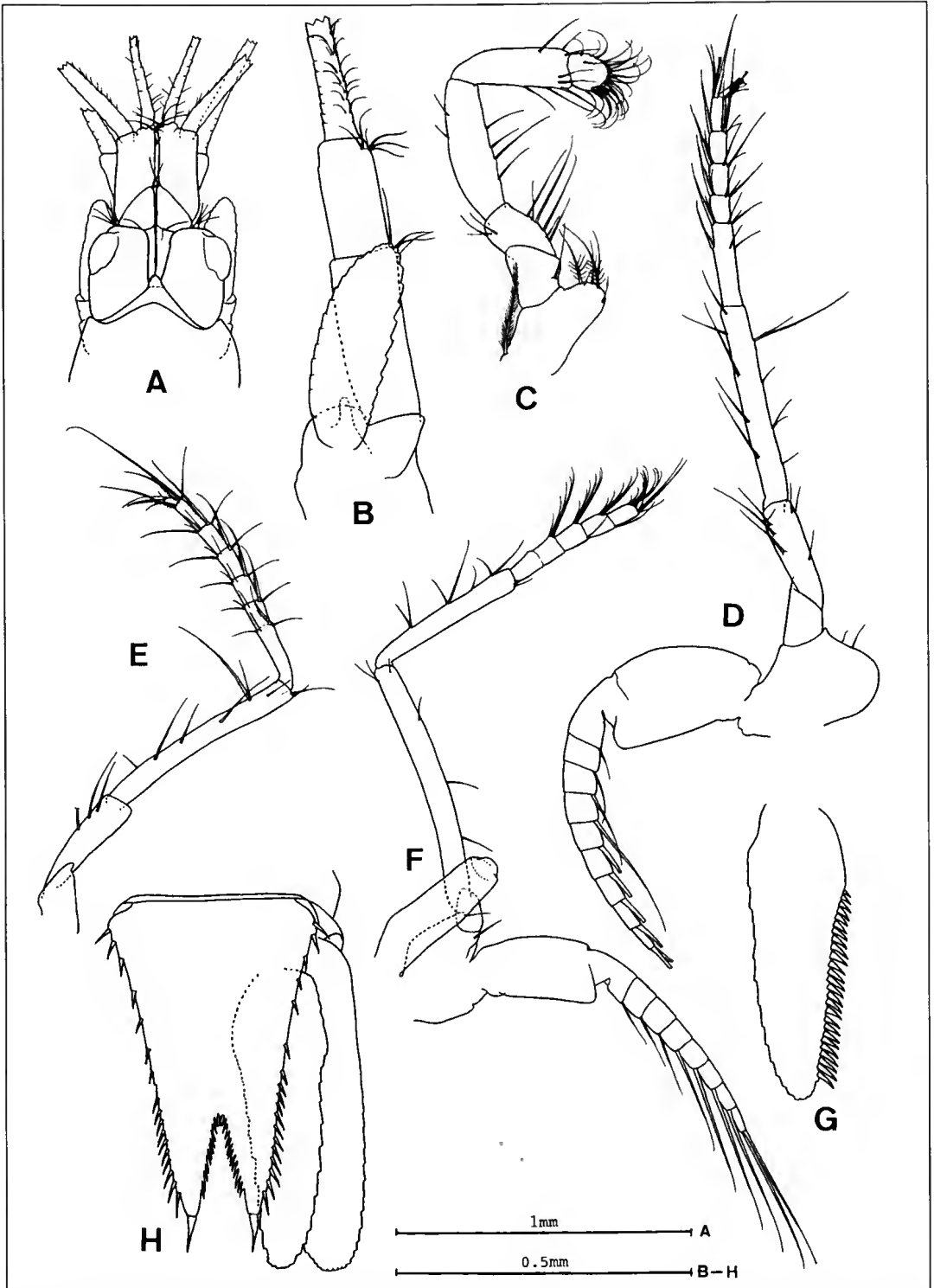


Fig. 6. *Heteromysoides sahalensis* sp. nov., holotype. **A**, anterior end of body; **B**, antenna; **C**, endopod of second thoracic limb; **D**, fourth thoracic limb; **E**, endopod of fifth thoracic limb; **F**, eighth thoracic limb and penis; **G**, endopod of uropod; **H**, uropod and telson.

three subsegments, subsegment 1 with one thick plumose seta and one slender seta on middle and distal corner of inner margin, subsegment 2 with one thick plumose seta and one barbed seta at inner distal corner, subsegment 3 with one thick seta and one short seta; dactylus small, with slender claw (Fig. 4G). Thoracic endopod 4 same as endopod 3 in structure but somewhat bigger, segmentation becoming more distinct (Fig. 4H). Thoracic endopods 5 and 6 very slender; ischium 1.1 times longer than merus; merus 1.25 times longer than 5-segmented carpopropodus (Fig. 5A, B). Thoracic endopod 7 very slightly bigger than endopod 8, both same as endopods 5 and 6 in structure but considerably smaller; ischium about 1.5 times longer than merus; merus 1.1 times longer than 4-segmented carpopropodus (Fig. 5C, D). Marsupium composed of two pairs of oostegites.

Abdominal somite 1 longer than somite 2; somites 2–5 subequal; somite 6 1.5 times longer than somite 5. Pleopods uniramous, unsegmented, increasing in length posteriorly, pleopod 5 is 1.8 times longer than pleopod 1.

Uropod setose all round; endopod extending beyond telson for 1/3 length of endopod, about four times as long as broad in statocyst region, medial margin nearly straight, without spines; exopod extending very slightly beyond endopod, about 4.5 times as long as greatest width (Fig. 5E).

Telson slightly longer than abdominal somite 6, 1.6 times longer than broad at base; lateral margin straight, with four pairs of spines increasing in length distally; distal margin slightly concave, with two pairs of spines, outer pair more than twice length of inner pair, equal to distalmost spine on lateral margin (Fig. 5E).

Remarks. As far as I can determine, six species of the genus *Heteromysoides* are now known: *H. cotti* (Calman, 1932), *H. spongicola* Bacescu, 1968, *H. longiseta* Bacescu, 1983, *H. dennisi* Bowman, 1985, *H. berberae* Bacescu and Müller, 1985, and *H. macrops* Murano, 1988. The new species resembles *H. dennisi* Bowman, 1985, collected from a cave off Grand Bahama Island, in the telson lacking an apical cleft, and the absence of spines on the uropodal

endopod, but is readily distinguishable from the latter species in the eye: *H. dennisi* bears an eyestalk produced into an acute process at the distolateral corner and the cornea occupying the central half of the lateral surface.

The thoracic endopod 3 in the new species does not develop a subchelate structure and closely resembles endopod 4 in structure. This is a conspicuous character, because all other species of the genus are known to have a subchelate termination in thoracic endopod 3, except for two species, *H. spongicola* and *H. macrops* for which it is not described.

Etymology. The species is named after the small body size.

Heteromysoides sahuensis sp. nov.

(Fig. 6)

Type specimen. HOLOTYPE – adult male, NTM Cr. 012278, 3.4 mm, Sahul Shelf, from 12°17.3'S, 129°40.9'E to 12°17.2'S, 129°41.8'E, 49–52 m, 24 June 1972, plankton net installed at mouth of beam trawl during RV *Hakuho Maru* Cruise KH-72-1.

Description. Carapace produced anteriorly in short triangular rostral plate with rounded apex, lateral margin of rostrum convex, leaving eyes and antennular peduncles uncovered (Fig. 6A); anterolateral corner of carapace rounded; posterior margin emarginate, exposing last thoracic somite dorsally.

Eye rectangular, large, extending to distal margin of antennular peduncle segment 1; cornea small, located at outer distal corner, not extending beyond anterior margin of eyestalk (Fig. 6A).

Antennular peduncle slender; segment 1 with outer distal corner produced anteriorly, tipped with several setae; segment 2 short, obliquely connected with segment 3, armed with two setae at inner distal corner; segment 3 more than twice as long as broad, armed with three setae at inner distal corner and one seta on inner margin (Fig. 6A).

Antennal peduncle shorter than

antennular peduncle (Fig. 6A), slender, segment 2 is 2.5 times as long as maximum breadth, equal to combined length of segments 1 and 3 (Fig. 6B). Antennal scale short, not reaching distal end of antennular peduncle segment 2, three times as long as broad, with convex inner margin and straight outer margin; setose all round (Fig. 6B).

Thoracic endopod 2 robust; endite from basis large; dactylus short, slightly longer than broad, with rounded apex armed with setae (Fig. 6C). Thoracic endopod 3 missing in this specimen. Thoracic endopod 4 with carpopropodus slightly longer than merus and 5-subsegmented, subsegment 1 slightly shorter than combined length of three intermediate subsegments (Fig. 6D). Thoracic endopod 5 with carpopropodus subequal to merus and 6-subsegmented but first articulation imperfect (Fig. 6E). Thoracic endopod 6 lost in this specimen. Thoracic endopods 7 and 8 more slender than endopods 4 and 5; carpopropodus longer than merus, 6-subsegmented, subsegment 1 longer than sum of succeeding segments (Fig. 6F). Thoracic exopods distal to basal plate 8- or 9-segmented (Fig. 6D, F).

Penis cylindrical, with rounded apex (Fig. 6F). Thoracic somites without sternal processes. Male pleopods uniramous, unsegmented, not modified, with developed side lobe, increasing in length from first to fifth pair. Uropod setose all round; endopod furnished with 26 spines arranged densely on inner margin from statocyst region to near apex (Fig. 6G); exopod equal in length to endopod (Fig. 6H).

Telson longer than last abdominal somite, 1.5 times as long as maximum breadth at base; lateral margin slightly concave in proximal half and slightly convex in distal half, armed with 18 rather slender spines arranged densely in distal half and sparsely in proximal half; each apex armed with single strong spine; distal sinus V-shaped, 1/3 as long as telson, furnished with 24 spinules on margin except distal short distance (Fig. 6H).

Remarks. The new species is easily distinguished from all the known species in: (1) both rami of the uropod equal in length, (2) the endopod of the uropod armed densely

with 26 spines on the inner margin from the statocyst region to near the apex, (3) the sinus of the telson is 1/3 as long as the telson and furnished with 24 spines on the margin, (4) the apices of the telson furnished with one spine each, and (5) the lateral margin of the telson armed with 17–18 spines on the entire length.

Etymology. The species is named after the locality in which it was collected.

ACKNOWLEDGMENT

I wish to express my sincere thanks to Dr. A.J. Bruce for giving me the opportunity of examining the specimens of the first two species.

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Accepted 20 March, 1997

GEOGRAPHIC VARIATION IN SCALATION AND SIZE OF THE BLACK WHIP SNAKES (SQUAMATA: ELAPIDAE: *DEMANSIA VESTIGIATA* COMPLEX): EVIDENCE FOR TWO BROADLY SYMPATRIC SPECIES

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ABSTRACT

The systematics and nomenclature of the black whip snakes have been the subject of lengthy and complex discussion. Examination of 512 specimens in Australian museums, including type specimens, shows that there are two species in the complex: *Demansia papuensis* (Macleay, 1877) and *D. vestigiata* (de Vis, 1884). When sexual dimorphism is taken into account, they are readily distinguished by scalation, size and to a lesser extent, colour, and are broadly sympatric in northern and north-eastern Australia. The smaller species with fewer ventral and subcaudal scales, *Demansia vestigiata*, is more broadly distributed, reaching south-eastern Queensland and southern coastal New Guinea. Despite the name, *D. papuensis* is not known with certainty from New Guinea.

KEYWORDS: Squamata, Elapidae, *Demansia*, Australia, systematics, geographic variation, sexual dimorphism

INTRODUCTION

Of the Australian elapid fauna, the whip snakes (*Demansia*) remain one of the most taxonomically confusing groups, despite over a century of investigation. Even if one ignores early controversy as to the limits of the genus (Worrell 1961a; Mengden 1983), there has been little agreement on the number of species and the names applied to them. One cause of much of the uncertainty has been a lack of material, with morphologists using small samples, unsure of the relevance of minor differences in coloration and scalation (Storr 1978). One aspect of this confusion has been systematics of the black whip snakes of northern Australia and New Guinea, the largest members of the genus.

Krefft (1869) first recorded large whip snakes with lengths of over a metre, assigning material to two species, *Diemenia psammophis* (Schlegel, 1837) and *Diemenia olivacea* (Gray, 1842) and providing a coloured drawing of the latter.

During the next 15 years, two names were proposed for large whip snakes, *Diemenia papuensis* Macleay, 1877, thought to be

from New Guinea, and *Diemenia atra* Macleay, 1884a, from Ripple Creek, Ingham, north Queensland, although neither description provided comparisons with other taxa.

Boulenger (1896) recognised the same two species of large whip snake as Krefft, placing *D. papuensis* in the synonymy of *D. psammophis*, and *D. atra* tentatively in the synonymy of *D. olivacea*. This nomenclature was largely followed by Kinghorn (1929), who also recognised *atra* as a distinct variety of *D. olivacea*, and provided coloured drawings of each species.

Within the next 30 years, two additional names were synonymised with *D. olivacea*: *Hoplocephalus vestigiatus* de Vis, 1884, by Mack and Gunn (1955) and *Diemenia maculiceps* Boettger, 1898, by Loveridge (1934).

The first large series of large whip snakes (n = 35) was amassed by Thomson (1935) from Cape York, who considered only a single species, *D. olivacea*, was represented. Thomson first applied the common name black whip snake to these snakes, although some authors used the common name spotted-headed snake (Kinghorn 1929; Glauert 1950).

Loveridge (1934, 1949) and Kinghorn (1942) were unable to consistently distinguish whip snake species, and suggested that only a single species with several subspecies was involved. This suggestion was not adopted by most subsequent authors. Glauert (1950) recognised *D. olivacea* in Western Australia as a distinct species from the Kimberley. Worrell (1952, 1956, 1961a-b, 1963) with the benefit of field experience with whip snakes in sympatry, also recognised *D. olivacea* as a distinct large species, demonstrating osteological differences between it and *D. psammophis* (Worrell 1956). He initially followed Kinghorn in recognising *atra* as a subspecies of *olivacea* from eastern Queensland (Worrell 1952), although later editions of the same work did not recognise subspecies (Worrell 1961b). He was also critical of Boulenger's synonymies, and transferred *D. papuensis* to the synonymy of *D. olivacea*, therefore re-identifying New Guinean populations as *D. olivacea* (Worrell 1961a-b).

These changes in the species name of New Guinean whip snakes were mirrored by Slater's (1956, 1968) alternative treatments, although in both cases he treated the New Guinea populations as a distinct subspecies, *papuensis*, as did Klemmer (1963). McDowell (1967) and Cogger (1971) referred large whip snakes from northern Australia and New Guinea to *Demansia olivacea*, without recognising subspecies.

A new nomenclatural complication was added by Cogger and Lindner (1974), who critically re-examined the identity of *Demansia olivacea* in the light of their collections from the type locality, Port Essington, and concluded that the name should be applied to the much smaller species previously known as *Demansia ornateiceps* (Macleay, 1878). They resurrected *D. atra* from synonymy for the black whip snake in Australia, but applied the name *D. papuensis* to New Guinean *Demansia*, noting the arbitrary nature of this action. Cogger and Lindner reported examining only one specimen of *D. atra* in their study.

Storr (1978) revised the *Demansia* of Western Australia, and examined limited additional material from the Northern Territory and Queensland. He reported a bimodal distribution in ventral and subcaudal scale counts in black whip snakes over a large part of the Kimberley and the Top End of the Northern Territory, and concluded for the first time that two broadly sympatric species were represented. The smaller species he identified as *D. atra*, referring to it specimens from Western Australia, the Northern Territory and Queensland. The larger species he described as *D. papuensis melaena*. In recognising this taxon as distinct, Storr considered *D. papuensis* a New Guinean species. He diagnosed his taxon as subspecifically distinct on the basis of differences in ventral counts and coloration, but did not report examining any specimens of the nominate subspecies. Storr's later comparative data (Storr *et al.* 1986), however, agree closely with Macleay's description of the holotype of *D. papuensis*. Storr also re-identified the specimen previously identified as *D. atra* by Cogger and Lindner (1974) as *D. papuensis melaena*, and noted differences between eastern and western populations of *D. atra*. While Storr's study was a major advance on previous results, it did not take into account the potential for sexual dimorphism, which could result in similar patterns of variation in scalation and size.

Parker (1982) followed Storr's nomenclature in referring New Guinean populations to *D. papuensis*, but suggested that more than one species may be present in New Guinea.

Shine (1980) identified *D. papuensis* from Cape York, from a single ovigerous female with larger eggs than *D. atra* (Shine 1985). Additional records of *D. papuensis* from eastern Australia were provided by Wilson and Knowles (1988) and Ingram and Raven (1991), the former authors assigning this population to the nominate subspecies without providing any supporting evidence. This identification was followed by Ehmann (1992) and Golay (1993), while Wells and Wellington (1985) considered *D. papuensis* to be restricted to New Guinea, and *D.*

melaena a distinct Australian species. Storr *et al.* (1986) were more cautious, merely identifying the Cape York population as 'some form' of *D. papuensis*.

In a final nomenclatural twist, Ingram (1990) established that the description of *Hoplocephalus vestigiatus* de Vis just predated that of *Demansia atra*, and hence used the combination *Demansia vestigiatus*, since adopted by Hutchinson (1990) and Golay (1993) as *Demansia vestigiata*, but not by Cogger (1992) and most other subsequent authors, who have continued to use *Demansia atra* as the available name for this taxon.

Thus, in summary, there remain disagreements as to the number of taxa of black whip snakes, their distribution, particularly in eastern Australia, and the nomenclature of the taxa. Few authors have reported examining type specimens. This paper resolves many of these problems by examining for the first time all available specimens in Australian museum collections, including type specimens, taking sexual dimorphism and geographic variation into account.

MATERIALS AND METHODS

Specimens ($n = 512$) were examined from the following collections: Australian Museum, Sydney (AM); Australian National Wildlife Collection, CSIRO Division of Wildlife Research, Canberra (ANWC); Museum of Victoria, Melbourne (MV); Museum and Art Gallery of the Northern Territory, Darwin (NTM); Queensland Museum, Brisbane (QM); South Australian Museum, Adelaide (SAM); Western Australian Museum, Perth (WAM).

Moderate to large specimens were identified as black whip snakes on size and coloration: consistent lack of a transrostral streak; consistent absence of dark nape bands and dark markings on the chin shields; usually dark venter; usual lack of a dark, pale-edged teardrop marking caudoventral to the eye, and usual presence of either dark caudal edges to the more cranial ventrals or a dark dorsum (Storr 1978). Small individuals, in which the adult coloration

was less developed, were also differentiated from other similar-sized *Demansia* by the proportionally very large eye and immature genital tract.

Where possible, all individuals were sexed by gross examination of gonads (testes or ovaries) and accessory ducts (epididymides or oviducts). The gonads were able to be differentiated even on very small individuals when well preserved. For some females carrying oviductal eggs, length and width of one or more eggs was measured with dial calipers.

Snout-vent length (SVL) was measured against a steel rule (50 cm or 1 m). Ventral and subcaudal scales were counted, using the Dowling method (McDowall 1967). Proportional measurements of head shields of small samples were made with an ocular micrometer on a dissecting microscope, to study claims by Boulenger and Storr of the relevance of scale shape to *Demansia* systematics. Head shield nomenclature follows McDowall (1967).

Simple statistical tests were performed with a hand calculator, while regressions and analysis of covariance were performed with the SYSTAT statistical package. In all analyses of scalation and size, sexes were treated separately. The superscripts *, **, *** indicate statistical significance at <0.05 , <0.01 and <0.001 levels of probability respectively.

RESULTS

Ventral scales. Two largely discrete groups of ventral counts are present in Australia, in both males and females (Table 1). In males, there is no overlap (high counts [group A] 199–228; low counts [group B] 169–191). Among females, there is a similarly bimodal distribution with slightly less separation (Group A 198–222; Group B 167–197), only three individuals having counts between 193 and 199 inclusive. These three individuals are clearly assignable to their respective groups on the basis of subcaudal counts and coloration (see below).

The two groups share a wide longitudinal range (Fig. 1). In both sexes, there is a statistically significant easterly trend,

towards higher values in group A (males: $\text{ventrals} = 0.71 \cdot \text{longitude} + 117.4$, $F_{1,64} = 52.384^{***}$; females: $\text{ventrals} = 0.46 \cdot \text{longitude} + 147.8$, $F_{1,57} = 19.199^{***}$), and lower values in group B (males: $\text{ventrals} = 195.1 - 0.10 \cdot \text{longitude}$, $F_{1,191} = 4.689^*$; females: $\text{ventrals} = 253.5 - 0.52 \cdot \text{longitude}$, $F_{1,78} = 40.383^{***}$), resulting in the greatest separation of ventral scale counts in the east (analysis of covariance: slopes: males $F_{1,255} = 62.849^{***}$; females $F_{1,135} =$

51.158^{***}). However, within each group, no sharp discontinuity in the longitudinal cline is evident.

In New Guinea and on Torres Strait islands, only values within the range of Australian group B are found (Table 1; Fig. 2).

Subcaudal scales. When examined without consideration of locality and ventral count, subcaudals in males show a less distinct bimodal distribution, while females do not show a bimodal distribution, although

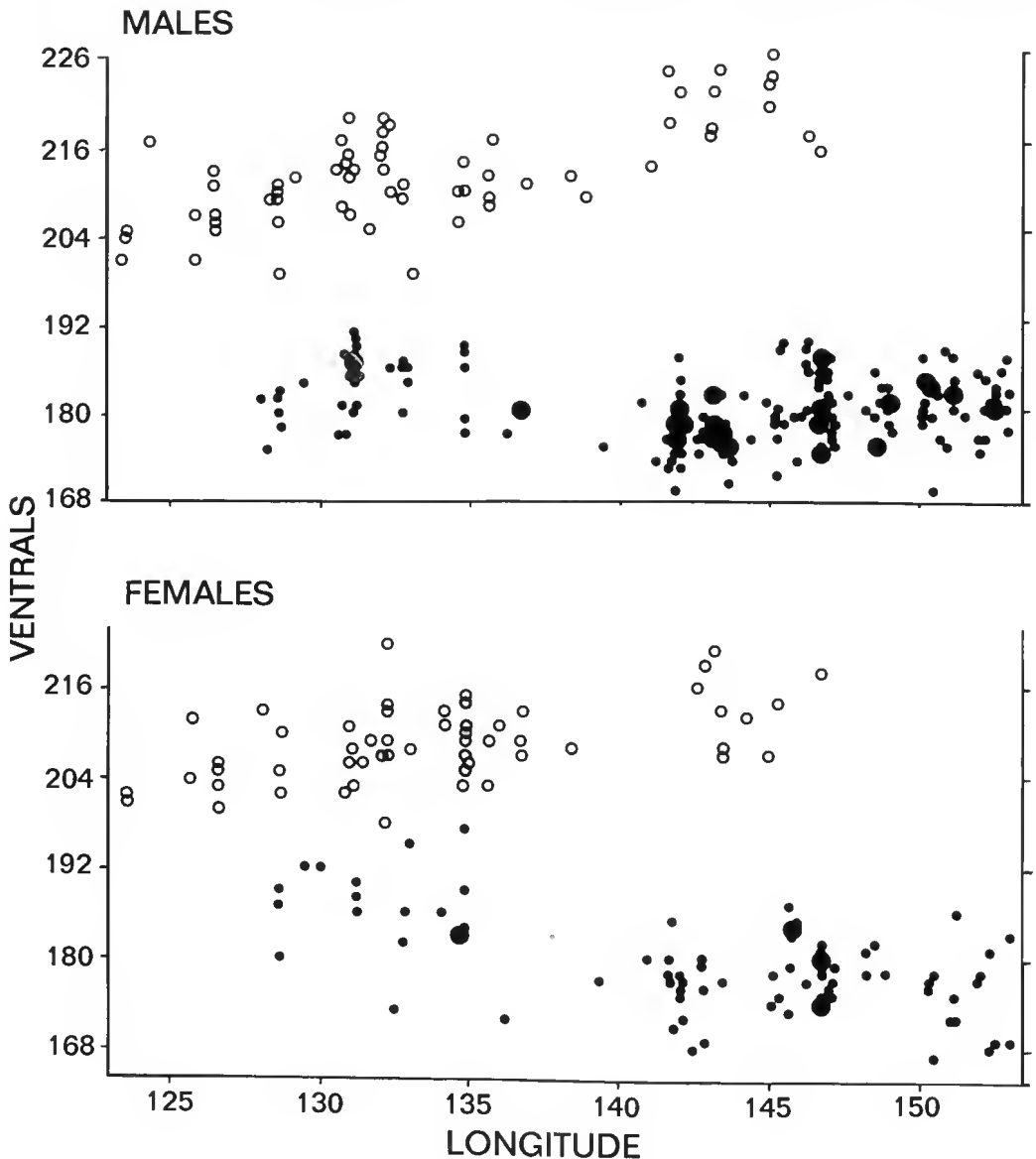


Fig. 1. Longitudinal variation in number of ventral scales in black whip snakes. Open circles are group A, dots are group B. Larger symbols represent multiple data points.

there are several peaks towards the high and low ends of the range. However, when individuals in the two groups of ventral counts are identified, a clear differentiation into two groups of subcaudal counts is obvious (Table 2): animals in group A consistently have high subcaudal counts while animals in group B consistently have low subcaudal counts. The differences between the group means are highly significantly different within sexes (males: $t_{239} = 20.55^{***}$; females: $t_{126} = 17.14^{***}$). Within groups and sexes, there is a statistically significant positive relationship between number of subcaudal and ventral scales (group A: males: $F_{1,56} = 26.935^{***}$; females: $F_{1,50} = 31.559^{***}$; group B: males: $F_{1,181} = 26.680^{***}$; females: $F_{1,73} = 9.999^{**}$).

Again, the greatest distinction between the two groups is in eastern Australia (Fig. 3), and only group B values are found in New Guinea and the Torres Strait islands (Table 2).

Snout-vent length. The two groups identified on the basis of scale counts differ noticeably in size, as represented by SVL (Fig. 4). In both groups, males are much longer than females, both in maximum and mean values (group A: males 26.5–154.5 cm, $n = 69$; females 25.9–124.5 cm, $n = 62$;

group B: males 16.4–108.0 cm, $n = 210$; females 19.5–92.6 cm, $n = 93$). The lengths are significantly different between sexes within each group (Wilcoxon Two-Sample Test, group A: $z = 2.040^*$; group B: $z = 7.124^{***}$). Group A animals are significantly longer than group B animals (Wilcoxon Two-Sample Test, males: $z = 5.079^{***}$; females: $z = 6.867^{***}$), with the difference apparent in all parts of the shared distribution, but most obvious in the east, where the largest adults of group A and the smallest adults of group B occur (Fig. 4). It is possible that the apparently larger size of eastern group A animals may be an artifact of collecting, with very large individuals being under-collected in the west. Evidence for this comes from sex ratio data. In group B, males are much more frequently collected than females (ratio 210:93; against a null hypothesis of equality, $\chi^2 = 44.4^{***}$). A non-significant trend towards a male skew is apparent in the Qld sample of group A (17:11; $\chi^2 = 0.893$, n.s.), while no clear trend is apparent in the WA and NT sample of group A (50:47; $\chi^2 = 0.041$, n.s.). If large animals are under-collected, then the larger males of group A should be collected less commonly than the small males of group B.

Table 1. Variation in ventral scale counts of black whip snakes.

	Males				Females				Total (including unsexed)			
	Range	\bar{x}	sd	n	Range	\bar{x}	sd	n	Range	\bar{x}	sd	n
Group A	199–221	213.0	6.80	68	198–222	209.2	5.24	62	198–228	211.3	6.36	137
Group B												
(Australia)	169–191	180.1	4.54	210	167–197	179.3	6.01	92	165–197	179.9	5.11	326
(Torres St)	172–182	178.2	3.77	5	177			1	172–182	178.4	3.31	7
(New Guinea)	174–182	177.6	2.35	12	174–182	177.2	2.78	10	174–182	177.4	2.45	23

Table 2. Variation in subcaudal scale counts of black whip snakes.

	Males				Females				Unsexed	
	Range	\bar{x}	sd	n	Range	\bar{x}	sd	n	Range	n
Group A	80–107	95.9	6.44	58	78–97	87.6	4.96	53	80–105	6
Group B										
(Total)	66–92	80.3	4.52	183	63–86	72.9	4.65	75	63–86	24
(Australia)	66–92	80.4	4.51	162	63–86	72.9	4.27	62	63–86	20
(Torres Strait)	77–83	80.0	3.00	3	80–84			2	80	1
(New Guinea)	70–85	79.5	5.75	11	64–76	70.6	4.00	8	70–75	2

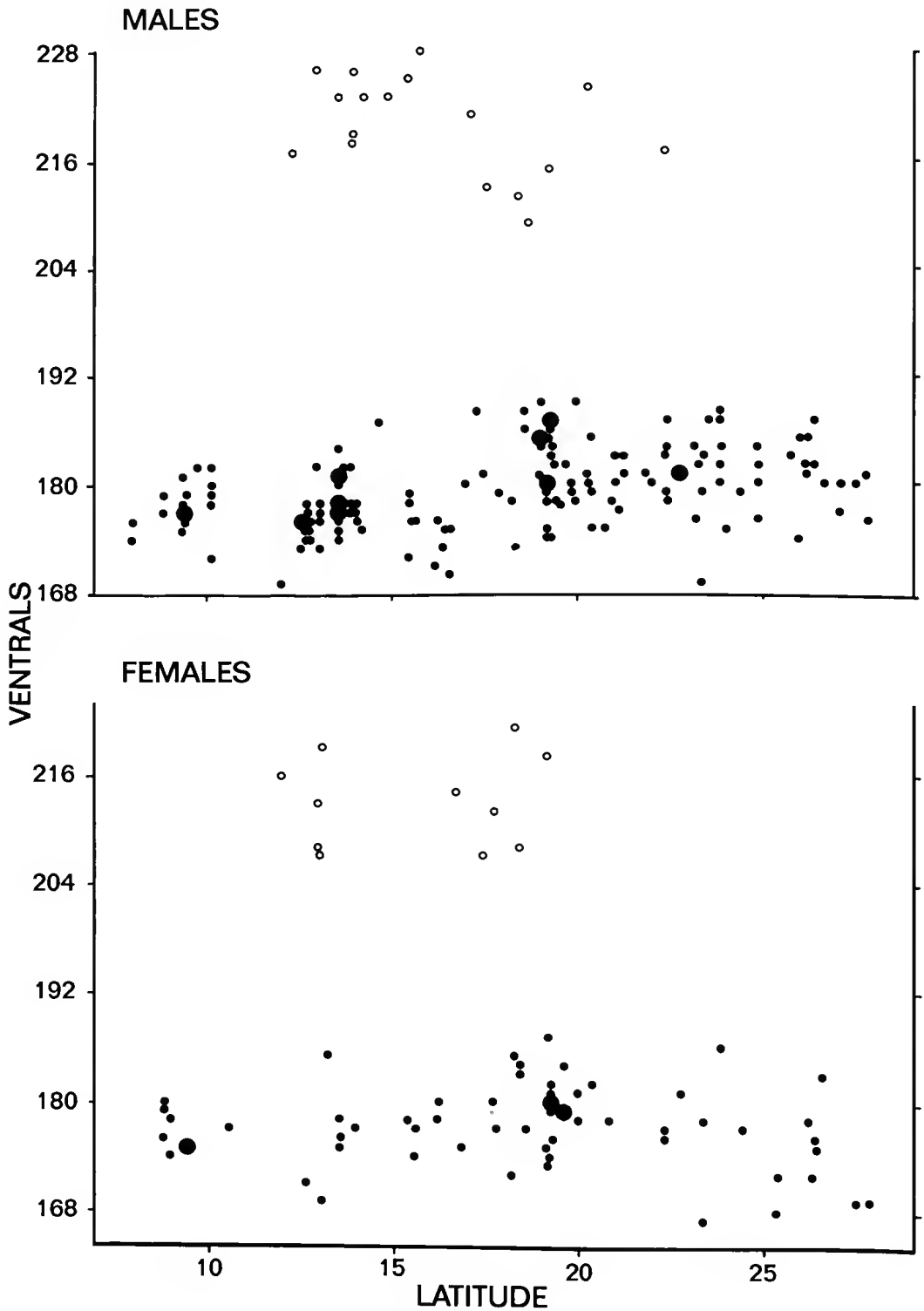


Fig. 2. Latitudinal variation in number of ventral scales in black whip snakes from the east of the distribution (Queensland and New Guinea). Open circles are group A, dots are group B. Larger symbols represent multiple data points.

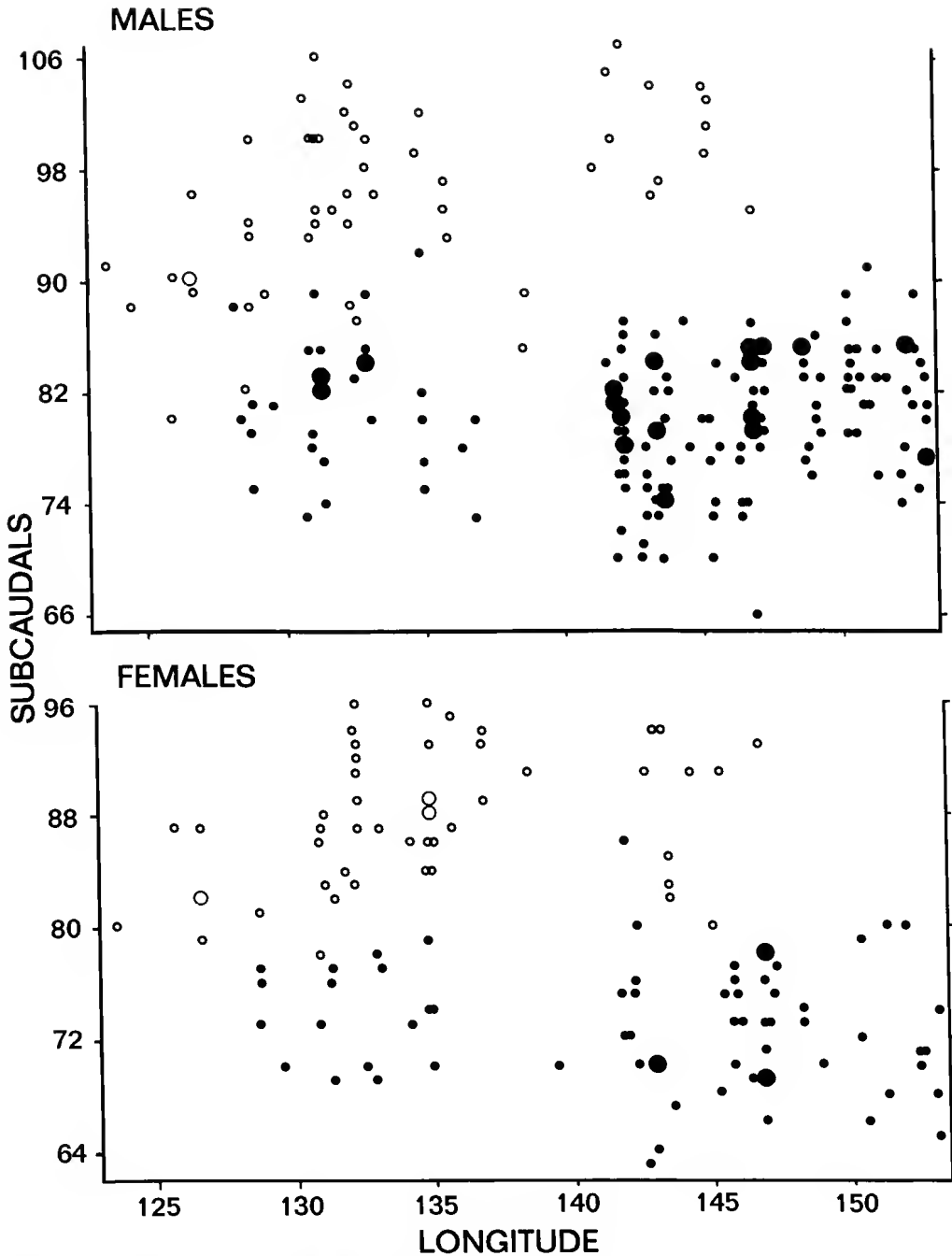


Fig. 3. Longitudinal variation in number of subcaudal scales in black whip snakes. Open circles are group A, dots are group B. Larger symbols represent multiple data points.

The difference in size between group A and B is also apparent at minimum size. The smallest (unsexable) individual of group A has SVL 22.8 cm, while 16 individuals of group B are shorter, with SVL as low as 16.4 cm.

An estimate of size at maturity is available for females from the smallest reproductively active female. For group A, the smallest of 18 females with oviductal eggs or enlarged ovarian follicles has SVL = 78.5 cm, while

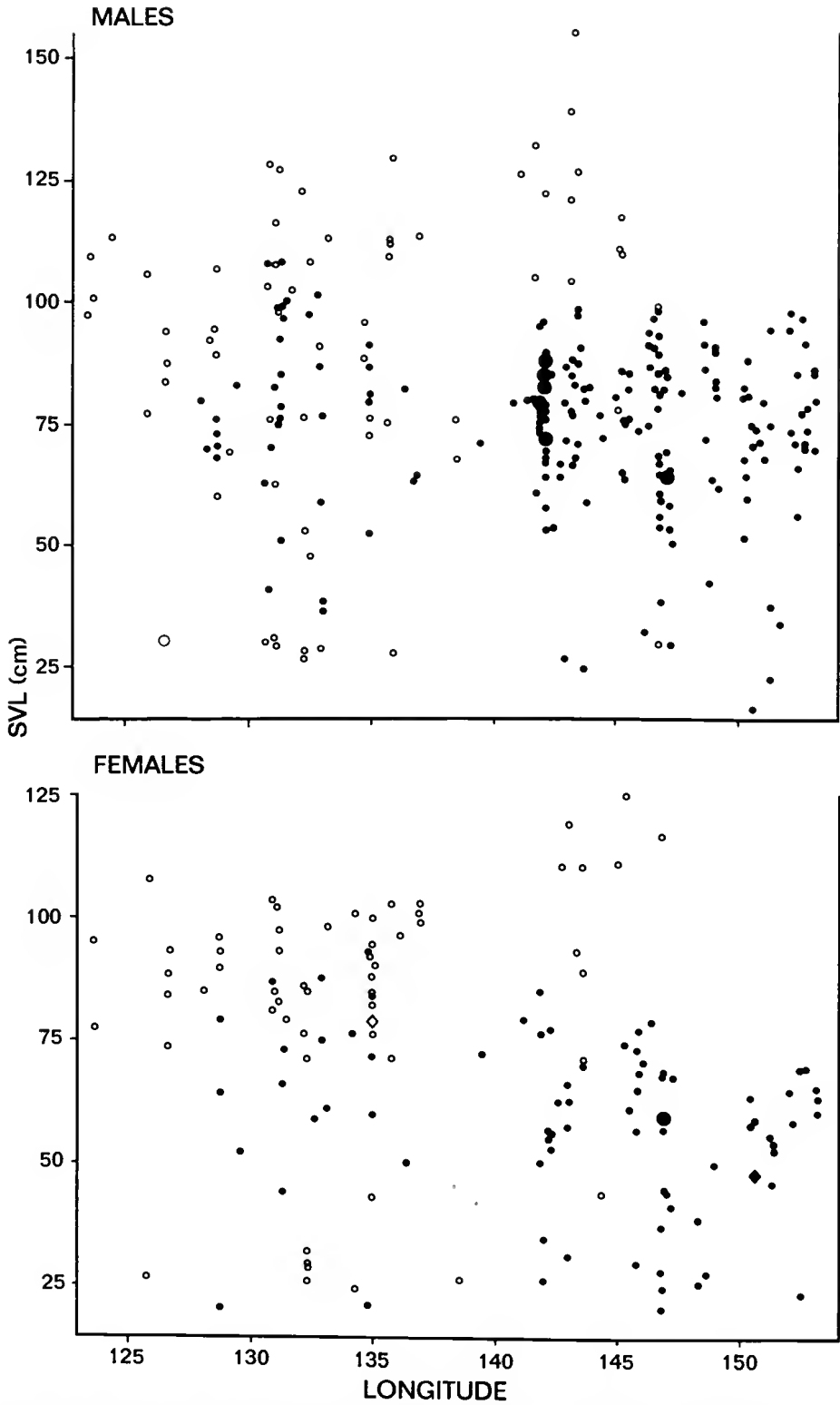


Fig. 4. Longitudinal variation in snout-vent length in black whip snakes. Open circles are group A, dots are group B. Larger symbols represent multiple data points. Open and closed diamonds indicate the smallest reproductively-active females in each group.

in group B, nine reproductive females have SVL from 47.8 to 78.7 cm.

The New Guinea specimens examined are all small, with the largest of the 23 measureable snakes (AM R86833, male) having SVL = 80.8 cm. Parker (1982) records maximum total length for individuals in the Western District as about 1 m, and reports a gravid female from this area with total length = 51.1 cm.

Coloration. Coloration differences between groups A and B are apparent, but not completely exclusive of each group.

Group A adults usually have a tan head, often with varying numbers of small dark spots or flecks, both dorsally and laterally. In some individuals, the spots are enlarged, in extreme cases merging to produce a coarse variegation over the head (e.g., NTM R16624). The orbit usually has a narrow, indistinct, broken pale margin. Cephalic markings in group B adults consist of varying expression of moderate to large dark blotches on the dorsal head shields, most extensive in eastern populations, a similarly broken narrow pale rim to the orbit, and often dark apical margins to scales in the temporal region. Some individuals have a short dark 'teardrop' marking caudoventral to the orbit, but not reaching the oral margin. The throat in both forms is immaculate.

Differences between adults of the two groups are also apparent in dorsal markings. In many group A adults, the dorsum is uniform, either dark slate to black (most western individuals, and some eastern individuals) or, less commonly, a lighter brown. Some individuals have dark bases to dorsal and lateral scales, particularly on the nape, but rarely dark apices. In most group B adults, the dorsal and lateral scales on the neck have dark apices, while the more caudal dorsal and lateral body scales are either evenly dark, or have dark bases. Geographic variation in the intensity of the dark markings on body scales is apparent, with many (but not all) adults from the extreme south-east, beyond the range of group A, having only dark bases to otherwise greenish dorsal and lateral scales. In both groups, the tail and caudal third of the body is often red-brown.

In group A, the ventral scales of the throat are usually cream, although some very large adults have traces of dark markings along the caudal margins of the scales. The ventral scales on the body are variably pigmented, from large dark blotches, often laterally positioned, to uniform dark pigmentation. All adults of group B have a well-defined dark caudal edge to the cranialmost ventral scales, which are usually yellow, while the more caudal ventral scales are generally uniformly dark (occasionally ventrals dark only laterally, e.g., QM J44971). In both groups, the tail venter is usually pale, with variable dark blotchy pigmentation.

Both groups show ontogenetic shifts in coloration, with juveniles uniformly pale green-brown and immaculate.

Both groups possess well-defined pale rectangular bars on the craniodorsal and cranioventral margins of body scales of all rows but the most ventral, concealed when the scales overlap, but exposed when the skin is stretched. The bar on the craniodorsal margin is shorter than its partner. The skin between the scales is also pale. These concealed markings are present throughout the genus (Storr 1978).

Egg size. From group A, single representative shelled eggs were measured from five ovigerous females (QM J8122, J50555, MV DT-D86, DT-D117, DT-D133) and a full clutch of eight eggs from one female (WAM R74045). The five former eggs have lengths and widths 48.2x17.2 mm, 28.6x13.0 mm, 52.5x11.7 mm, 30.0x14.1 mm and 30.5x12.2 mm (width/length ratio 0.223–0.470). The eight latter eggs have length 35.2–42.9 mm (\bar{x} = 40.3, sd = 3.39) and width 13.1–16.5 mm (\bar{x} = 15.3, sd = 1.09), with width/length ratio of 0.308–0.469 (\bar{x} = 0.383, sd = 0.051).

From group B, two full clutches of eight eggs (NTM R3433, WAM R74045) were measured. The former clutch has length 26.0–35.5 mm (\bar{x} = 29.5, sd = 2.89), width 10.0–12.0 mm (\bar{x} = 11.6, sd = 0.68), and width/length ratio 0.338–0.462 (\bar{x} = 0.394, sd = 0.036), while the latter has length 26.7–32.6 mm (\bar{x} = 29.2, sd = 1.85), width 14.4–17.5 mm (\bar{x} = 16.5, sd = 0.939) and width/length ratio 0.515–0.616 (\bar{x} = 0.567, sd = 0.033).

Thus, while widths of eggs are similar in the two groups, some group A eggs are considerably longer than group B eggs.

Head scalation. Head scalation shows minimal variation. What variation is present is apparently due to individual anomalies. In samples of 20 individuals from each of the two groups, representing all parts of the geographic range, the following scalational features occur at least unilaterally on 90% or more of each: rostral about as tall as wide, triangular when viewed from in front; internasals in broad contact, nearly square or a little broader than long; prefrontals in broad contact, longer than broad and longer than internasals; supraoculars about twice as long as broad, about as broad as frontal; each parietal bordered by two temporals and four to five occipitals, the rostralmost occipital largest; nasal completely divided by a large nostril, the two resulting segments about the same length, but rostral part much taller, both segments contacting internasal, caudal segment contacting prefrontal; preocular taller than long, with a prominent canthus rostralis in adults, contacting nasal, prefrontal and supraocular; postoculars two, about equal in size, dorsal postocular contacting supraocular, parietal and primary temporal, ventral postocular contacting primary temporal and supralabials; primary temporal single; secondary temporals between parietal and last supralabial two, lowermost overlapping last supralabial; temporolabial distinct (not fused to last supralabial, *contra* the illustrations of Storr *et al.* 1986), large, deeply wedged between last two supralabials, and narrowly separated from lip; supralabials six, first contacting rostral and nasal, second contacting nasal and preocular, third contacting preocular and entering orbit, fourth entering orbit and contacting lower postocular, fifth contacting lower postocular, primary temporal and temporolabial, sixth contacting temporolabial and lower secondary temporal; caudalmost extremity of fifth supralabial occasionally split off to form a small additional supralabial; infralabials seven, first pair oblique, in broad contact at the mental groove, second pair small, squarish, separated by pregenials; pregenials shorter than postgenials.

The most common deviations from this pattern are extension of the lower postocular to contact the parietal, and extension of the temporolabial to contact the postoculars rostrally or the oral margin ventrally.

Length and width of the frontal shield were measured on slightly larger samples. In 35 specimens of group A, the width/length ratio is 0.416–0.612 (\bar{x} = 0.491, sd = 0.041), while in 137 specimens of group B, it is 0.382–0.595 (\bar{x} = 0.490, sd = 0.041).

Distribution and sympatry. There is broad geographic overlap in tropical Australia between the two groups (Fig. 5), although group A extends generally further inland and west. Group B is more strictly coastal, and extends further to the south-east. Both forms are found together at a number of localities, with the largest samples from Milngimbi Mission, in the Crocodile Islands (n = 11 in group A, 8 in group B), the lower Archer River, in Cape York (n = 1 in group A, 15 in group B), and Townsville (including the suburbs Cranbrook, Mudginburra, Gulliver and Pallarenda and James Cook University; n = 2 in group A, 21 in group B). At each of these three localities, the distinction between the two groups in counts, size and coloration is maintained. Among group B in Australia, one locality is considered erroneous, and another suspect. SAM R1102 is purportedly from 'Minnie Downs', Qld, presumably the station of that name in south-western Qld, very distant from other localities. Given the lack of confirmatory records from this region, I ignore this record. QM J37052 has the locality 'west of Anakie, Qld'. This is further inland than other records at this latitude, and given the imprecise locality, is possibly in error or based on a transported specimen.

In New Guinea, where only group B is definitely recorded, all specimens but one are from the south side of the central cordillera (Fig. 6), and from close to the coast in two regions: the Fly River delta and around Port Moresby. The exception is ANWC R1014, a head and tail from Maprik (East Sepik district). Until confirmatory records are available from this region, I regard this locality as erroneous.

Both forms occur on several offshore islands. Group A occurs on Bathurst and Milngimbi Islands along the Northern

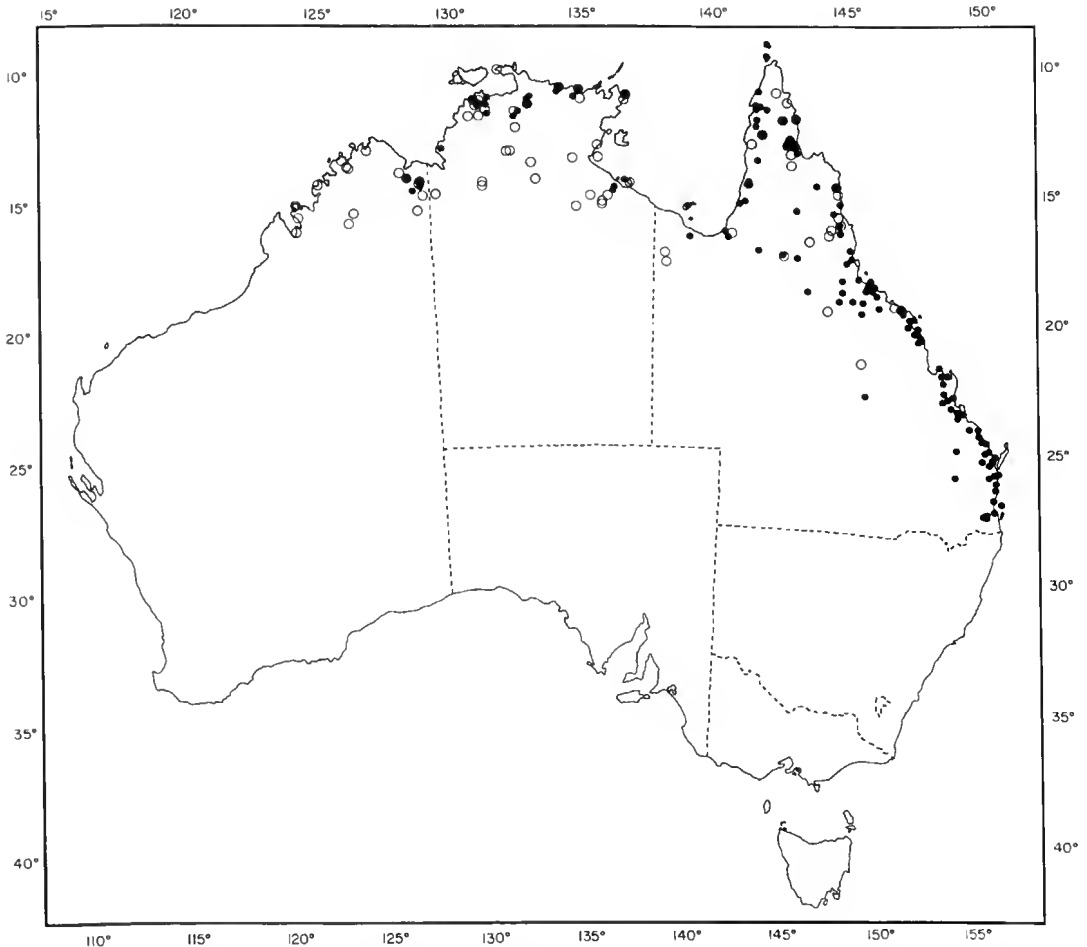


Fig. 5. Distribution of black whip snakes in Australia. Open circles are group A (*D. papuensis*), dots are group B (*D. vestigiata*).

Territory north coast, and Vanderlin and Maria Islands in the south of the Gulf of Carpentaria. Group B occurs on Badu and Thursday Islands in Torres Strait, Milingimbi Island along the Arafura Sea coastline, Centre and Mornington Islands in the south of the Gulf of Carpentaria, and Magnetic, Rabbit and North Stradbroke Islands along the Queensland east coast.

Type specimens. *Diemenia papuensis* was described by Macleay (1877) from a single specimen. There is some doubt about the type locality. Macleay (1877) stated that the specimen was simply labelled New Guinea, and suggested that it was collected at Hall Sound by the *Chevert* Expedition. The locality Hall Sound has since been

considered the type locality by most authors (Goldman *et al.* 1969; Cogger 1979; Cogger *et al.* 1983). The holotype (AM R31919, male; formerly Macleay Museum R713; Figs. 7, 8A) is in poor condition, soft and very faded (based on Macleay's description of a much darker coloration and traces of darker tint in non-exposed areas), missing much of the stratum corneum of the scales, and with the vertebral column broken at midbody. It has 222 ventrals, is missing the tail tip, but has 88 subcaudals up to the missing portion, and SVL 129.0 cm (Macleay gives 225 'abdominals', 88 subcaudals, and SVL 51 inches). The left postgenial is malformed, either developmentally or through injury, and the

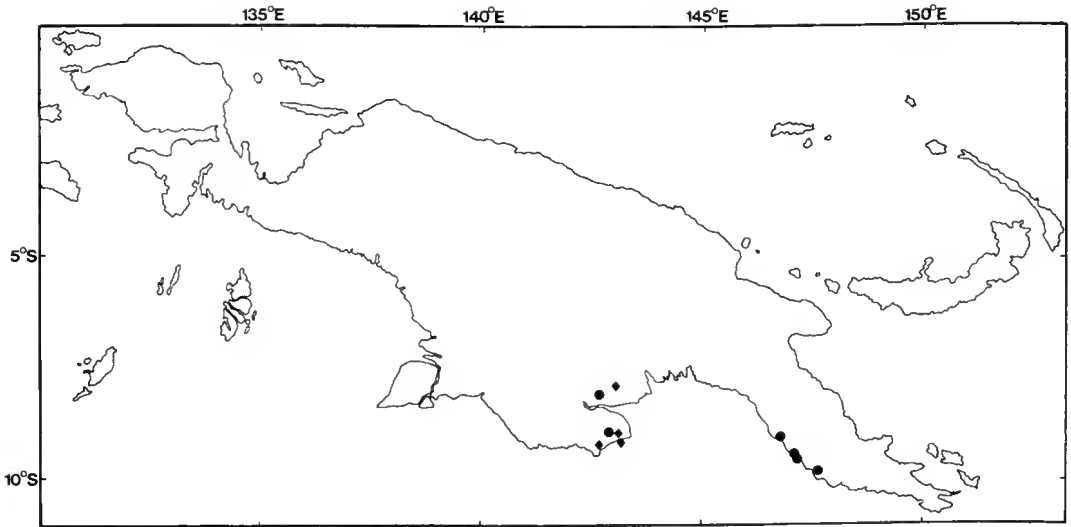


Fig. 6. Distribution of group B black whip snakes (*D. vestigiata*) in New Guinea. Dots are specimens examined; diamonds indicate additional localities cited by Parker (1982).

nasal is narrowly separated from the preocular. On the basis of size and ventral scale count, and the relatively large number of subcaudals, it is clearly referable to group A. However, this form is not otherwise known from New Guinea. Given the lack of precision of the type locality, the fact that the *Chevert* Expedition also collected at two Australian mainland localities (Cape Grenville and Somerset), and that the Macleay collection, during the period preceding Macleay's paper, received other collections from both Cape York Peninsula and New Guinea (Macleay 1875; Tilbrook 1992; S. Norrington, pers. comm.), I believe it likely that the recorded type locality is incorrect.

Hoplocephalus vestigiatus de Vis, 1884, was described from a damaged specimen from an unknown locality. The original description gives 152 ventrals, but lacks a subcaudal count and measurements. Corrections to the description were presented by Mack and Gunn (1955), who give 182 ventrals. The holotype, QM J206 (Figs 8B, 9), is soft, lacks large patches of stratum corneum on head and body, with some of the exposed areas dried and distorted, has the throat torn, and is missing much of the tail. It has 184 ventrals, SVL 60.6 cm, head dorsum with dark blotches, nape scales with dark apices and dark-edged

ventrals on the throat. In all respects, it is a member of group B.

Diemenia atra Macleay, 1884a, was described from a collection received from J.A. Boyd of Ripple Creek, Ingham. No indication was given of the number of specimens on which the name was based, although only a single set of measurements and counts was presented. Two specimens have been identified as types: one (R131727; formerly B5941), presented to the Australian Museum by Macleay in 1885 as a type, the second (AM R31920, formerly Macleay Museum R708) originally in the Macleay Museum collection, identified on jar labels as a type. Of these two specimens, R31920 (Figs. 8C, 10) agrees more closely with Macleay's description (180 ventrals, 68 subcaudals, SVL 31 inches), and was designated lectotype by Wells and Wellington (1985). AM R31920 is a female with 177 ventrals, 69 subcaudals, SVL 78.5 cm, and the temporolabial bilaterally reaching the lower postocular, while AM R131727 is a male with 186 ventrals, 78 subcaudals and SVL 90.4 cm. Both lectotype and paralectotype are members of group B on scalation and size, and agree with this group in coloration (dark-edged ventrals on throat, body venter and dorsum uniform black). The locality given for both types in museum registers is Herbert River, which

Macleay (1884b) had used as an alternative description of the collector's residence.

Diemenia maculiceps was described from a single female specimen collected by Richard Semon from the Burnett River (Boettger 1898; Mertens 1967). I have not examined the holotype (Senckenberg Museum, Frankfurt 20498), but photographs and notes on coloration made by Dr H.G. Cogger (pers. comm.) clearly indicate that the type has the coloration of group B, in particular no transrostral bar, large dark blotches on the head shields and dark apices to scales on the nape. Further, the type locality is only within the known range of group B.

The holotype of *Demansia papuensis melaena* Storr, 1978 (WAM R47590; Figs 8D, 11), is a non-reproductive adult female from Katherine Farms, NT, collected by G. Gow. It has 211 ventrals, 85 subcaudals and SVL 101.7 cm, an evenly dark dorsum, small dark flecks on the head, and lacks dark

margins to the more anterior ventrals, and is clearly a specimen of group A.

TAXONOMIC CONCLUSIONS

The concordance of variation in scalation, size and to a lesser extent coloration, together with the wide geographic overlap between the two forms, with morphological distinction maintained in sympatry, argues for the occurrence of two species. Geographic variation in each species is apparently continuous. On mainland Australia, there is no evidence for any population being either geographically isolated or consistently morphologically different, while New Guinea and Torres Strait island populations are morphologically completely consistent with the smaller Australian species. Thus, I do not recognise subspecies within either species. The earliest available name for the larger species with high scale counts (group A) is *Diemenia papuensis*, with *Demansia papuensis melaena* a junior synonym. The earliest available name for the smaller species with low counts (group B) is *Hoplocephalus vestigiatus*, with *Diemenia atra* and *Diemenia maculiceps* as junior synonyms. Although *D. vestigiata* has only recently and inconsistently been used as the available name for this taxon, *D. atra* has only been in use for the same taxon since 1974, prior to which the species was widely known as *D. olivacea*. I do not consider that use of the binomen *Demansia vestigiata* will cause nomenclatural instability any greater than the unavoidable confusion resulting from the restriction of *D. papuensis* to Australia.

The two taxa are most readily differentiated on ventral counts: 165–197, rarely above 193, for *D. vestigiata*, 198–228 for *D. papuensis*.

IDENTITY OF MATERIAL DISCUSSED BY PREVIOUS AUTHORS

The taxonomic conclusions of this paper differ from the many solutions presented by previous authors. Many of the specimens

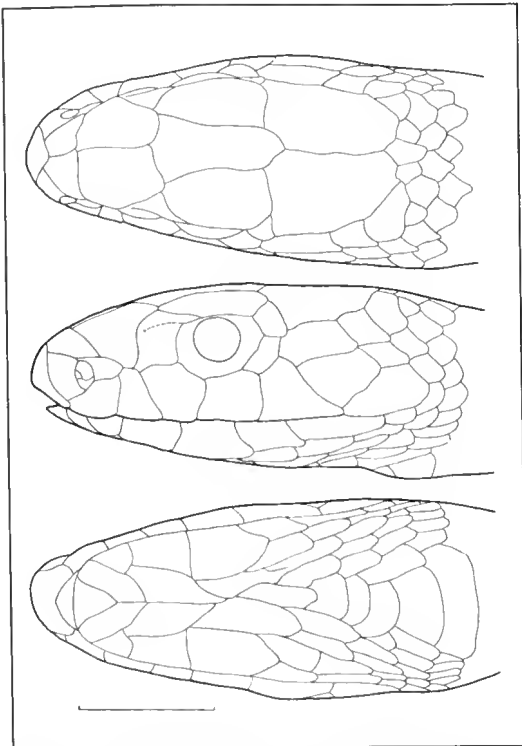


Fig. 7. Dorsal, lateral and ventral views of the head shields of the holotype of *Diemenia papuensis*. Scale bar = 10 mm.

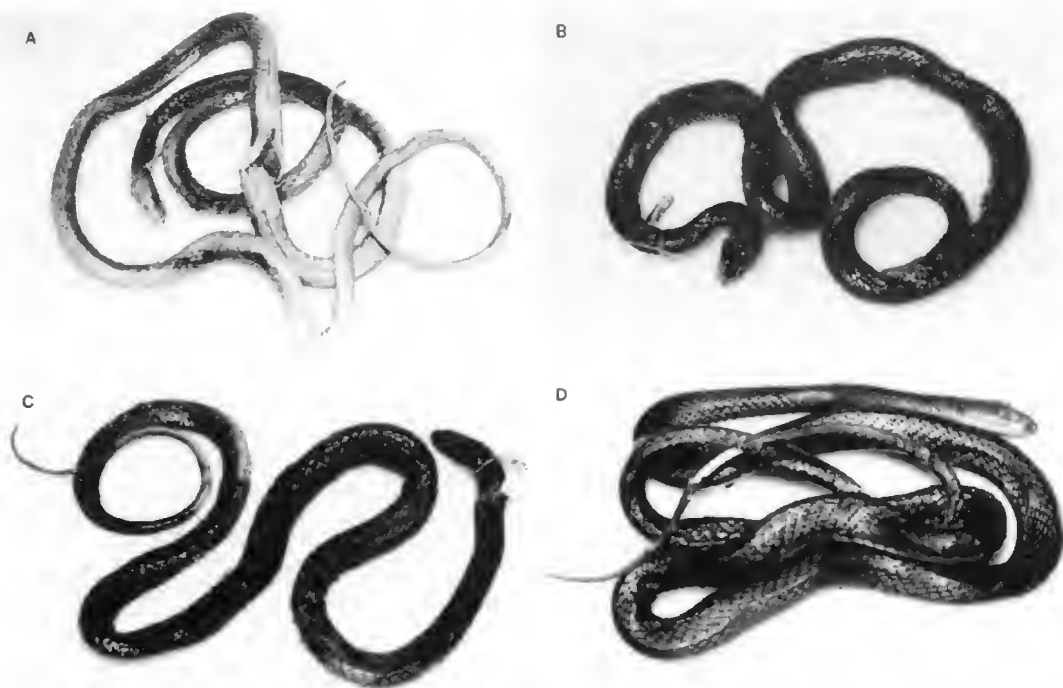


Fig. 8. A, holotype of *Diemenia papuensis*; B, holotype of *Hoplocephalus vestigiatus*; C, lectotype of *Diemenia atra*; D, holotype of *Demansia papuensis melaena*.

examined for this paper were also utilised by these earlier workers, and it is now possible to re-identify some of the material used in these studies.

Krefft (1869) reported specimens of *Diemenia psammophis* and *D. olivacea* from Port Denison. One large early specimen of *D. papuensis* (AM R6097) is from Port Denison, and is likely to have been the basis of Krefft's record of *D. psammophis* from this locality, as the counts and measurements he gives roughly correspond with this specimen. From his description of *D. reticulata* as common around Sydney, Krefft clearly applied this name to true *D. psammophis*, and thus recognised this species as distinct from the large whip snakes.

Although none of the specimens used by Boulenger (1896) were examined in this study, the combination of locality and scale counts given allows the identification of many specimens. The New Guinea and Cape York specimens (Boulenger's a–d) of his variety B of *D. psammophis*, in which he

placed *D. papuensis*, are clearly *D. vestigiata*. However, at least the second (f) of his Port Essington specimens of this 'variety' is *D. papuensis*. The other specimens (e, Port Essington; g, Daly River) may be *D. vestigiata* or *D. olivacea*. Among Boulenger's specimens referred to *D. olivacea*, a, b (north-eastern Australia) are most likely *D. vestigiata*, c (Port Darwin) may be *D. vestigiata* or *D. olivacea*, and d (Port Essington) is *D. papuensis*.

All of the specimens in the D.F. Thomson collection, now in the Museum of Victoria, were examined. The Cape York *D. olivacea* reported by Thomson (1935) are a mixture of *D. papuensis* and *D. vestigiata*.

Among the Worrell material lodged in the Australian Museum and Museum of Victoria as '*D. olivacea*' are specimens of *D. papuensis* from Mataranka (AM R13229, R13231), and one of *D. vestigiata* (MV D8626) from central Qld. As noted by Storr (1978), the only specimen of '*D. atra*' listed by Cogger and Lindner (1974) is a *D. papuensis*.

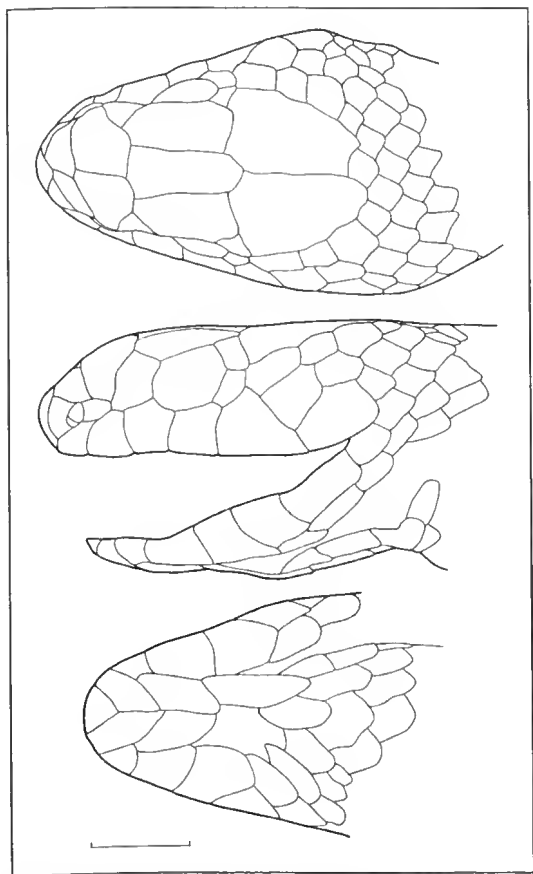


Fig. 9. Dorsal, lateral and ventral views of the head shields of the holotype of *Hoplocephalus vestigiatus*. Scale bar = 5 mm.

With the exception of WAM R47684 (Koolan I.), all specimens identified as *D. papuensis* and *D. vestigiata* (as *D. atra*) by Storr (1978) I consider correctly identified. The exception is a member of the *D. olivacea* complex, not *D. papuensis*. Further, three small individuals (WAM R21937, R24928, Katherine; R45688, 'Mt House') that Storr assigned to *D. olivacea* I re-identify as juvenile *D. papuensis*, hence including the central Kimberley in the range of this species for the first time.

Shine's (1980) account of the ecology of *D. atra*, based on the dissection of Australian Museum and Queensland Museum material, is clearly from a composite sample of *D. papuensis* and *D. vestigiata*, with the range of SVLs covering both taxa. However, the specimen he identified as *D. papuensis* (QM J8122) is correctly identified.

Thus, it is now clear that most previous studies were working with composite samples, usually small. This study emphasises the importance of examining large samples and using a range of collections to resolve taxonomic problems in snakes.

SPECIMENS EXAMINED

Demansia papuensis. AM R258, King Sound, WA; R3780, MV D4507, Pt Darwin, NT; AM R6097, Pt Denison, Qld; R9928, MV DT-D136, Roper River, NT; AM R10422, Cooktown, Qld; R13229, R13231, Mataranka, NT; R14033, Forrest River Mission, WA; R19105, R41869, Maningrida, NT; R20199, S of Katherine, NT; R31919, ?New Guinea (holotype of *Diemenia papuensis*); R41095, WAM R47590 (holotype of *Demansia papuensis melaena*), Katherine Farms, NT; AM

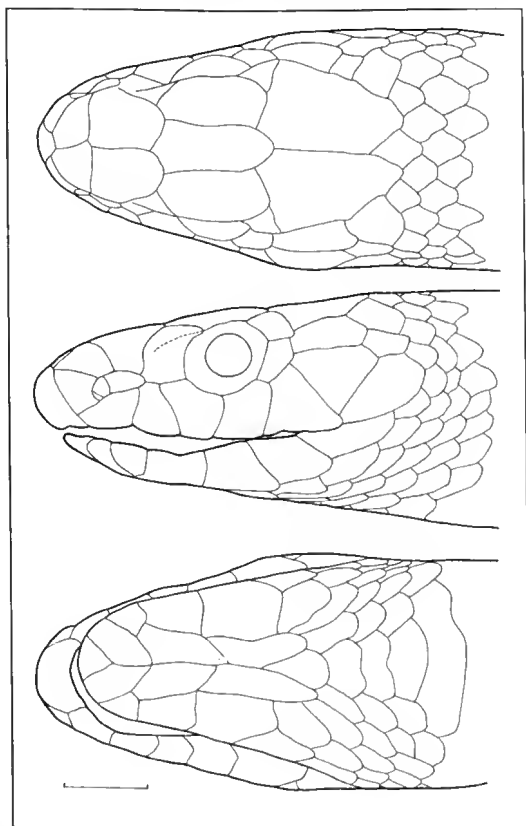


Fig. 10. Dorsal, lateral and ventral views of the head shields of the lectotype of *Diemenia atra*. Scale bar = 5 mm.

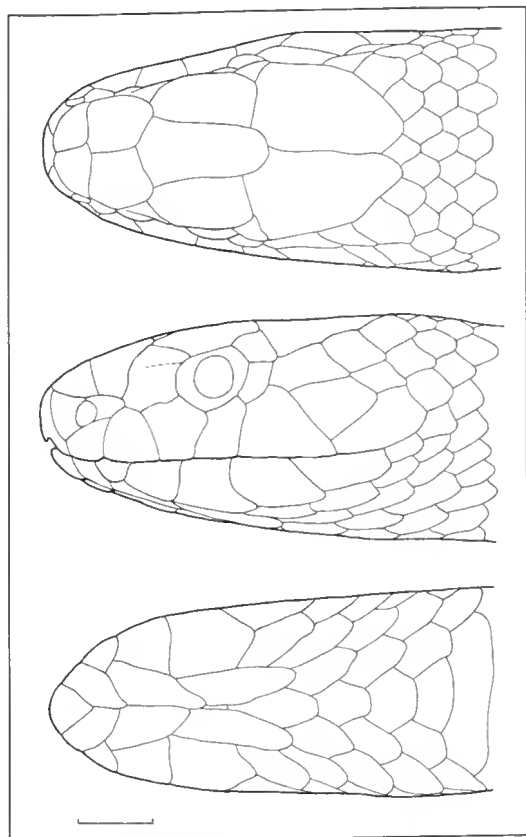


Fig. 11. Dorsal, lateral and ventral views of the head shields of the holotype of *Demansia papuensis melaena*. Scale bar = 5 mm.

R63378, 27.3 km E Georgetown, Qld; R79146, 8 km E Mareeba, Qld; R88831, Jabiluka Project Area, NT; R119699, Dimbulah, Qld; R139881, 11 km W Kununurra on Wyndham Rd, WA; R142895, 1 km W October Ck, NT; ANWC R543, between Mary River and South Alligator River on Cooida Rd, NT; R810, Numbulwar, Rose River, NT; R818, corner of McMillans Rd and Rapid Creek Rd, Rapid Ck, NT; R825, Tayimi, Bathurst I., NT; R946, Caranbirini Waterhole, 20 km NE Mimets Camp, NT; R1289, Mimets Base Camp, McArthur River, NT; MV R12811, QM J2976, Koolpinyah, NT; MV D8693-94, QM J33598, J50555, no locality; MV D10065-66, DT-D104-105, Roper River Mission, NT; R51889, Larrimah, NT; DT-D85, DT-D128, Yonko River, Qld; DT-D86-88, DT-D98-99, DT-D102, DT-D110, DT-D112, DT-D137-139, Milingimbi Mission, NT; DT-D106, Glyde River, NT; DT-D115,

lower Archer River, Qld; DT-D117, DT-D133, Yirrkala, NT; DT-D126, DT-D130, DT-D1168, DT-D1232, Bare Hill, Qld; NTM R156, R3720, Katherine Farms Rd, NT; R294, R5247, R16717, Howard Springs, NT; R2287, 9 mi W Katherine, Lower Farms Rd, NT; R3817, R3828, Katherine district, NT; R4727, Howard Springs Reserve, NT; R4729, R16775, WAM R16509, R21937, R23893, R23895, R24928, R26347, Katherine, NT; NTM R5814, Katherine, low level, NT; R5854, Berry Springs Reserve, NT; R6719, Ivanhoe Crossing, WA; R6882, Keep River, 35 km E WA border, NT; R7045, Kununurra, WA; R8266, El Sharana, NT; R8386, 11 km W Katherine on Stuart Hwy, NT; R9493, Victoria River by Victoria River Crossing, NT; R13149, Humpty Doo, NT; R14211, Vanderlin I., NT; R16575, R16621-22, R16624, R17234, Humpty Doo area, NT; R16823, 'Marrakai' Stn Rd, 5 km from Arnhem Hwy, NT; R17915, Jabiru East, NT; R20514, Cape Crawford area, NT; R20571, 'Bauhinia Downs', NT; R21008, Woolanang, NT; R32362, Berrimah, NT; R32369, Pine Creek, NT; R32370, R32372, Darwin, NT; R32373, Maria I., NT; NTM A/S R33, Gregory Ck, Qld; QM J2974, nr Pt Darwin, NT; J8122, Wenlock, Qld; J22344, Mt Molloy, Qld; J31513, Stoney Pt, Kungatham, nr Temple Bay, Qld; J33597, Pallarenda, Qld; J33599, 8 km S Elliot River between Bowen and Home Hill, Qld; J33600, Mudginburra, Qld; J38351, 'Silver Plains' HS, Qld; J39845, 1.5 km S Coen, Qld; J44972, 'Goldsborough', Lolworth Range, south face, Qld; J50269, Adel's Grove, 5 km E Lawn Hill NP, Qld; J50414, Lynd River, 'Amber', Qld; J51750, 20 km NE Coen, Qld; J51751, 60 km S Coen, Qld; J51230, Heathlands Rd, 2 km N 'Shelburne Bay' HS turnoff, Qld; J53825, Lockhart River, Qld; J54392, J54394, vicinity of Widdallion Ck, Qld; J57655, Musgrave-Pornpuraow Rd, Qld; J58745, Rossville, Qld; J58881, 13.8 km NE Normanton, Qld; J59377, Epping Forest, Qld; SAM R6640, Victoria River, NT; R29954, nr Humpty Doo, NT; WAM R144, Derby, WA; R11244, R12360, Wotjulum, WA; R11979-80, Kimberley Research Stn, WA; R13286-88, R22425, R28073, R64695-97, R125241-42, Kalumburu, WA; R13648, Wyndham, WA;

R22923, Kuri Bay, WA; R26673, Cape Don, NT; R45688, 'Mt House', WA; R46834, Prince Regent River Reserve, WA; R51202, Kimbolton Spring, WA; R51816, Stewart Range, 'Kimbolton', WA; R53714, Mitchell Plateau, WA; R55865-66, main dam site, Lake Argyle, WA; R60580, Camp Ck, Mitchell Plateau, WA; R74045, Gove, NT; R75125, 11 km W 'New Lissadell' HS, WA; R87272, 10 km NNE Kununurra, WA; R97960, nr Mt Barnett, WA.

Demansia vestigiata. AM R3335, MV D1936, D4430, D9016-17, NTM R3560, R16623, QM J206 (holotype of *Hoplocephalus vestigiatus*), J353, J1584-86, J19849-50, J47357, J50562, no locality; AM R5845, R31920 (lectotype of *Diemenia atra*), R131727 (paralectotype of *Diemenia atra*), QM J1593-94, Herbert River, Qld; AM R6205, Eidsvoll, Qld; R6488, Homebush, Mackay, Qld; R6938, Mackay district, Qld; R7611-12, Mekeo, 60 mi NW Port Moresby, PNG; R8906, Caloden Bay, Centre I., Pelew Is., NT; R9024, Coorooman, Qld; R12459-63, northern Australia; R14032, R14034, Port Keats Mission, NT; R14599, R14625, Laloki River, PNG; R16737, 'Silver Plains', Qld; R17079, Gregory Springs via Hughenden, Qld; R25823, R115352-53, QM J25884, J32903, Port Moresby, PNG; AM R30716, R66763, R93233, R121152, MV D14435, Wipim, PNG; AM R37868, 10 mi S Coen, Qld; R40276, Cannon Hill, NT; R40847, Tully, Qld; R40848, QM J26088, J40700, J48963, Gladstone, Qld; AM R44533, Karumba, Qld; R49833, R62738, Burnett Heads, Qld; R54201, Finches Bay, Cooktown, Qld; R54918, 30 km upstream, Liverpool River, NT; R55039, 3 km S Batten Pt, NT; R56661, 114 km N Cairns on Cooktown Rd, Qld; R56662, Annan River crossing, southeast of Cooktown, Qld; R57054, 5 mi S Gladstone, Qld; R59063, R59110, QM J37944, J43427-28, Badu I., Qld; AM R59888, 4 mi N Yalboroo on Bruce Hwy, Qld; R59889, 24 mi N Proserpine, Qld; R62018, about 20 km from Weipa on Mapoon Rd, Qld; R63727, Crooked Creek at Gulf Hwy, 34.5 km W Georgetown post office, Qld; R65905, Isis River crossing on Bruce Hwy, 13 km E Childers, Qld; R66211, QM J16821, Mitchell River Mission, Qld; AM R69971,

Kerry Head, Proserpine, Qld; R79262, ANWC R350, NTM R315, R32361, Beatrice Hill, NT; AM R81473, just below Ross River Dam, west of Townsville, Qld; R81474, rubbish tip *ca* 4.7 km W Cooktown post office via airport rd, Qld; R81475-76, Bowen tip, Qld; R82541, R85720, Lorim Pt, Weipa, Qld; R82559, abandoned Mapoon Aboriginal Settlement, north of Weipa, Qld; R82587, R82589, QM J52813, Thursday I., Qld; AM R84222, northeast Qld; R86833, Kapa Kapa, 50 mi SE Port Moresby, PNG; R88573, Jabiluka Project Area, NT; R91627, R94368, Weipa district, Qld; R92530, Ord River Diversion Dam, WA; R93715, Ross River, vicinity of Kelso, 14 km from Townsville, Qld; R97430, NTM R17913, Jabiru East, NT; AM R97515, Magela Crossing on Oenpelli Rd, 2 km N 'Mudginberri' Stn, NT; R97539, 1 km S Micca Ck crossing on Jim Jim Rd, NT; R105280, opposite end of airstrip, Coen Rd from Weipa, Qld; R107091, 11 km E Weipa on Coen Rd, Qld; R110339, R110359, R110374, QM J3638, SAM R12784, WAM R55615, Townsville, Qld; AM R111360, Berrimah Farm, NT; R112425, Arnhem Hwy, vicinity of Jabiru, NT; R113357, Mt Morgan tip, Qld; R114142, Maningrida, NT; R119456, Darwin, NT; R119698, Dinah Lagoon, Dinah I., Staaten River, Qld; R121994, Moitaka, Port Moresby, PNG; R127965, Mt Carbine, Qld; R141689, 8 km E South Alligator River on Arnhem Hwy, NT; ANWC R170, Mackay Harbour, Qld; R814, Humpty Doo Rd, between ricefields and CSIRO Stn, NT; R823, 1 mi NW Fogg Dam, Humpty Doo, NT; R1014, Maprik, PNG [in error]; R1421, Yeppen, 3 mi S Rockhampton, Qld; R2698, 30 mi S Rockhampton, Qld; R2784, Normanton, Qld; R5279, eastern Mellwraith Range lowlands, Qld; R5419, Shoalwater Bay Army Training Reserve (22°24'S 150°12'E), Qld; R5458, Shoalwater Bay Army Training Reserve (22°45'S 150°18'E), Qld; R5481, Shoalwater Bay Army Training Reserve (22°24'S 150°16'E), Qld; MV R12809, R12869, NTM R808, Oenpelli, NT; MV R12810, D8477, Darwin, NT; R12861, Cape York, Qld; D4672, D4732, D4825, PNG; D4681, Daintree River, Qld; D8684, QM J7573, J15878, Rockhampton, Qld; MV

D5903, Bora Bada, PNG; D8443, Mornington I., Qld; D8467, D8475-76, Finnis Lake, NT; D8626, central Qld; D8971, Cleveland, Qld; D49836, D49896, Awaba, PNG; DT-D89, DT-D97, DT-D100-101, DT-D103, DT-D111, WAM R13532-33, Milingimbi Mission, NT; MV DT-D90, nr Cape Direction, Qld; DT-D91-94, DT-D107, DT-D113-14, DT-D119, DT-D121-125, DT-D131, DT-D1169, lower Archer River, Qld; DT-D96, nr Pt Musgrave, Qld; DT-D95, QM J48122, Gympie, Qld; MV DT-D108, lower Archer River (register) or lower Watson River (label), Qld; DT-D109, second Red Rocky Point, Qld; DT-D127, lower Watson River, Qld; DT-D129, DT-D134-35, Katji Lagoon, NT; NTM R919, Mareeba, Qld; R987, Edward River Mission, Cairns, Qld; R1174, Berrimah, NT; R1940, Stuart Hwy, Berrimah, NT; R3433, 27.0 km E Mt Bundy turnoff on Arnhem Hwy, NT; R3452-53, Harrison Dam, 29 km NE Noonamah, NT; R6215, Gunn Point Rd, Howard Springs, NT; R8373, nr river, Howard Springs, NT; R12479, Fogg Dam, NT; R16620, R16625, Humpty Doo, NT; R16822, Adelaide River floodplain, Arnhem Hwy, NT; R17060, 2 km E Adelaide River on Arnhem Hwy, NT; NTM A/S R492-494, Borroloola, NT; QM J309, Brisbane, Qld; J359, Coongoola district, Colosseum, Qld; J374-75, Noosa Heads, Qld; J604, J7073, Cape York, Qld; J1595, Cardwell, Qld; J1782, Pt Darwin, NT; J2544, J22781, SAM R18625, Bundaberg, Qld; QM J2572-73, 30 mi E Darwin, NT; J3572, Belmont, Brisbane, Qld; J4195, Watalgan, Qld; J5677, Homebush Rd, Glendora, Mackay; J6948, Konedobu, Pt Moresby, PNG; J6954, Base area, lower level, PNG; J7864, J7871, J8123, Wenlock, Qld; J10028, Bucasia, nr Mackay, Qld; J10359, Atherton, Qld; J10710, J15810, J40344, Proserpine, Qld; J13445, Gulliver, Townsville, Qld; J13515, Toorbul, Qld; J13576, nr Townsville, Qld; J14335, 5 km S Iron Range, Qld; J14336-37, Browns Ck, Cape York, Qld; J17672, 26 km N Gladstone on Bruce Hwy, Qld; J18355, 9.6 km N Bundaberg on Rosedale Rd, Qld; J18535, 3.2 km S Tiara on Bruce Hwy, Qld; J20429, Mt Brisbane, Esk, Qld; J21791, J21797, J21783, Humpty Doo district, *ca* 64 km SE Darwin, NT; J21964, J25499, 'Pine Valley', Brooweena, Qld; J21970, Broadwater Ck, via Baffle Ck, Qld; J22033, Darwin area, NT; J22149, Mirani, Qld; J22300, J47301, Gympie district, Qld; J22577, 8 km W Woodgate, Qld; J22618, Pt Curtis Rd, Rockhampton, Qld; J23199, Millaroo, nr Ayr, Qld; J23213, Marina Plains - Musgrave, *ca* 10 km from Musgrave, Qld; J25698, Coolum, Qld; J26665, 26.1 km NW Townsville on Bruce Hwy, Qld; J28070, 0.5 km N Lockhart River, Qld; J28071, 2 km N Lockhart River, Qld; J28447, Mackeral St, Tin Can Bay, Qld; J28787, 2 km N Lockhart River community, Qld; J28789, nr school, Lockhart River community, Qld; J28909-10, 10 km SE Paluma turnoff on Bruce Hwy, Qld; J29082-84, Shoalwater Bay Army Reserve, Qld; J32286, Croydon, Qld; J32290, Shute Harbour, Qld; J32898, Korobosea, Pt Moresby, Qld; J33501, Toolara SE, Qld; J35171, Takura, nr Maryborough, Qld; J35172, Hervey Bay, Qld; J36033, Hervey Bay (urban), Qld; J36081, Booloomba Ck headwaters, Connondale Ranges, Qld; J37052, W of Anakie, Qld; J37581, J38213, Pt Stewart, Qld; J37584, Peach Ck, 16 km NE Mt Croll, Qld; J37585, Lankelly Ck, 10 km NE Coen, Qld; J37586, Rocky River, 8 km SW mouth, Qld; J37587, 3 km SE Coen, Qld; J37610, 5 km SW 'Breakfast Creek' HS, Qld; J39680, 8 km N Camp Beagle on Watson River Rd, Qld; J39844, York Downs, 50 km E Weipa, Qld; J40230, N of Camp Beagle, *ca* 40 km N Aurukun, Qld; J40279, Yaamba, Shoalwater Bay area, Qld; J40767, Cooktown, Qld; J40935, Harrisville, Qld; J41395, N Stradbroke I., Qld; J41530, Maryborough area, Qld; J44592, 'Warrawee', Qld; J44961, J44984, 'Toomba', Qld; J44971, J44982, 'Hillgrove', Qld; J44979, 'Southwick West', Qld; J44983, J44986, 'New Moon', Qld; J46811, junction of Catfish Ck and Calliope River, Qld; J46864, Fletcher Ck mouth, Burdekin River, Qld; J47297, Winfield via Gympie, Qld; J47410, Durong, Qld; J48663, 29 Ward St, Tewantin, Qld; J48681, Kinka Beach, N of Emu Park, Qld; J49836, Nelly Bay, Magnetic I., Qld; J49940, Boondoomba, via Proston, Qld; J50557-58, J50561, J50563-64, J50566-67, J50570,

J50575, Pallarenda, Townsville, Qld; J50559, Townsville Town Common, Qld; J50560, Pallarenda Rd, Pallarenda, Qld; J50565, Mt Elliot turnoff, S of Townsville, Qld; J50568, 'Jerona', S of Townsville, Qld; J50569, Cape Cleveland, Qld; J50571, J51978, 'Inkerman', Qld; J50572, Cranbrook, Townsville, Qld; J50573, Bohle River, Hervey Range Rd, Qld; J50574, Greenvale area, NW of Townsville, Qld; J50576, Mt Elliot, Qld; J52851, 11.2 km N Marceba, Qld; J52858, Gregory River, 16 km S Burketown, Qld; J53087, MacDonald Point, Shoalwater Bay, Qld; J53639, 1 km N site 12, Shoalwater Bay, Qld; J53640, Plot 11, nr site 12, Shoalwater Bay, Qld; J55227, Cape Hillsborough Rd, Qld; J55228, Rabbit I. NP, Qld; J57044, corner Sugarloaf and Strathdiekie rds, via Proserpine, Qld; J57098, 'Warrill View' (QDPI Animal Genetics Centre), Qld; J57654, 'Lochnager' outstation, Qld; J57656, 'Rutland Plains' HS, Qld; J58149, Peak Crossing, Qld; SAM R1102, 'Minnie Downs', Qld [in error]; R34265, Jabiru airstrip, NT; R34351, James Cook University, Qld; R35462-63, Kununurra, WA; WAM R10242, Ivanhoe, WA; R13448, Wyndham, WA; R13509, Yirrkala, NT; R22347-48, R29914, Kimberley Research Stn, N of Kununurra, WA; R25089, 60 km SSE Wyndham, WA; R55849, Routh Ck, 30 km E Georgetown, Qld; R56160, 2 km W Croydon, Qld; R57865, nr Laura, Qld; R71209, 10 km N Cooktown, Qld; R75539, 3 km SSE Kununurra, WA; R75552, 6 km NE Kimberley Research Stn, WA.

ACKNOWLEDGMENTS

I thank the following museum curators and collection managers for allowing me to examine specimens in their care: K. Aplin, P. Couper, J. Covacevich, J. Coventry, A. Edwards, P. Horner, M. Hutchinson, R. Sadlier, L. Smith, J. Wombey and the D.F. Thomson Management Committee. Dr H. Cogger kindly provided me with details of his notes on type specimens in European collections, while R. Sadlier allowed access to computing facilities. B. Jantulik prepared the final drafts of head drawings. Specimens

were examined during visits to interstate museums funded by an ARC Institutional Grant to the author. P. Couper, J. Covacevich, A. Greer and R. Shine kindly read and criticised the manuscript.

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Accepted 10 December, 1997

SIMOSELAPS MORRISI SP. NOV. (ELAPIDAE), A NEW SPECIES OF SNAKE FROM THE NORTHERN TERRITORY

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ABSTRACT

Simoselaps morrissi sp. nov. is a member of the semi-fossorial *S. semifasciatus* subgroup. Key distinguishing characters of the new species are a shovel-shaped snout tipped with a sharp cutting edge, combined ventral and subcaudal scale count of 159–161, diffuse to absent dark head blotch and non-banded body and tail. It is found in *Eucalyptus miniata* dominated woodland in northern Arnhem Land. A meristic variable for *S. incinctus* is revised.

KEYWORDS: Reptilia, Elapidae, *Simoselaps*, *morrissi*, *incinctus*, new species, Northern Territory, Australia

INTRODUCTION

The endemic genus *Simoselaps* Jan, 1859, is Australia's most speciose taxon of elapid snakes. Composed of small (<0.6 m total length), semi-fossorial species, the genus is characterised by the presence of prominent dark nuchal and head blotches and, in most species, numerous transverse bands on the body. *Simoselaps* is distributed throughout subhumid to arid areas of Australia (Wilson and Knowles 1988; Cogger 1992) and contains thirteen species (Hutchinson 1990).

Simoselaps has had a complex taxonomic history, having been dispersed among six genera (Mengden 1983; Hutchinson 1990). Hutchinson (1990) reviewed evidence for the probable monophyly of the genus and recognised: *S. anomala* (Sternfeld, 1919); *S. approximans* (Glauert, 1954); *S. australis* (Krefft, 1864); *S. bertholdi* (Jan, 1859); *S. bimaculata* (Duméril, Bibron and Duméril, 1854); *S. calonota* (Duméril, Bibron and Duméril, 1854); *S. fasciolatus* (Günther, 1872); *S. incincta* Storr, 1968; *S. littoralis* Storr, 1968; *S. minima* (Worrell, 1960); *S. roperi* (Kinghorn, 1931); *S. semifasciatus* (Günther, 1863); and *S. warro* (de Vis, 1884).

As an aid to identification, *Simoselaps* has been divided into four morphological subgroups (Wilson and Knowles 1988; Ehmann 1992). The *S. semifasciatus*

subgroup is the largest of these, containing species distinguished by a shovel-shaped snout tipped with a sharp cutting edge. Most members of this subgroup are oophagous (Scanlon and Shine 1988).

In the Northern Territory *Simoselaps* is most diverse in the arid centre, where six species occur (*S. anomala*, *S. bertholdi*, *S. fasciolatus*, *S. incincta*, *S. roperi* and *S. semifasciatus*). Only the banded *S. roperi* is known in the monsoonal wet/dry tropics north of 16° latitude.

Wilson and Knowles (1988) published a photograph of an unbanded *Simoselaps* from Nabarlek in western Arnhem Land, Northern Territory, which appeared to represent an undescribed species. In 1996 two specimens of the taxon became available for examination.

MATERIALS AND METHODS

A detailed morphometric and meristic analysis was made on two specimens of an undescribed species of *Simoselaps*, 21 specimens of *S. incinctus* and nine specimens of *S. warro*. A total of 16 meristic and mensural variables were recorded from each individual (Table 1). Measurements were made with electronic digital callipers and/or a steel rule. Counts of lateral head scales were made on both sides of the body.

Table 1. Comparison of morphometric and meristic characteristics of *Simoselaps morrissi* sp. nov., *S. incinctus* and *S. warro*. Measurements are in mm (SD = standard deviation).

Characteristics	<i>Simoselaps morrissi</i> sp. nov. n = 2			<i>Simoselaps incinctus</i> n = 21			<i>Simoselaps warro</i> n = 9		
	mean	SD	range	mean	SD	range	mean	SD	range
Snout-vent length (SVL)	234	48.08	200–268	258	40.64	185–330	282	33.04	218–325
Tail length 28.6 6.83	28.6	6.83	23.8–33.4	25.6	4.64	18.5–33.9	30.4	5.40	23.0–40.9
Body width	8.3	1.34	7.4–9.3	8.1	1.28	6.1–10.7	10.6	1.40	8.8–13.3
Head length	11.6	1.19	10.8–12.5	10.0	0.95	8.4–11.6	14.0	1.56	11.5–16.4
Head depth	5.1	1.05	4.3–5.8	4.5	0.41	4.0–5.5	5.7	0.81	4.7–7.2
Head width	7.7	1.32	6.8–8.7	6.3	0.67	5.2–7.4	8.2	0.99	6.9–9.4
Frontal length	3.1	0.45	2.8–3.4	2.6	0.19	2.3–3.0	4.3	0.51	3.4–5.0
Frontal width	2.7	0.28	2.5–2.9	2.5	0.24	1.9–2.9	2.7	0.23	2.4–3.2
Snout length	4.4	0.52	4.0–4.7	4.0	0.32	3.5–4.5	4.6	0.54	3.9–5.5
Postoculars cont. ant. temporal	1	0	1–1	2	0	2–2	2	0	2–2
No. of gular scale rows	5	0	5–5	6.4	0.90	5–8	5	0.71	4–6
No. of supralabials	6	0	6–6	6	0	6–6	6	0	6–6
No. of midbody scale rows	15	0	15–15	16.3	0.97	15–17	15	0	15–15
No. of ventral scales	140	2.12	138–141	163	8.78	145–178	141	8.69	129–157
No. of subcaudal scale	20.5	0.71	20–21	20.7	2.24	17–25	19.8	3.49	14–23
Total ventral + subcaudal scales	160	1.41	159–161	184	8.61	166–197	160.3	5.85	152–172
Percentages	12.2	0.42	11.9–12.5	10.1	1.58	7.0–11.9	10.9	2.41	7.4–14.2
tail length (% of SVL)	3.6	0.16	3.5–3.7	3.1	0.23	2.7–3.6	3.8	0.38	3.4–4.6
Body width (% of SVL)	5.0	0.52	4.6–5.4	3.9	0.39	3.4–4.8	5.0	0.40	4.4–5.7
head length (% of SVL)	2.2	0	2.2–2.2	1.8	0.18	1.5–2.2	2.0	0.26	1.5–2.5
head depth (% of SVL)	3.3	0.12	3.2–3.4	2.4	0.25	2.0–2.8	2.9	0.27	2.5–3.3
head width (% of SVL)	1.9	0.16	1.8–2.0	1.6	0.17	1.3–1.9	1.6	0.13	1.4–1.8
frontal length (% of SVL)	1.34	0.08	1.3–1.4	1.0	0.14	0.9–1.4	1.5	0.12	1.3–1.7
frontal width (% of frontal length)	87.7	3.70	85.1–90.4	94.3	8.42	70.8–106.0	65.0	5.00	58.3–72.2

Of the measurements and counts taken, the following require definition:

1. Snout length, measured as the distance from the anterior margin of the orbit to the tip of the rostral scale;
2. Body width, measured as the width of a ventral scale detached from the widest part of the body (Thorpe 1975);
3. Head length, measured as the distance between the tip of the rostral scale and posterior edge of the lower jaw (Thorpe 1975);
4. Head depth, measured at the deepest part of head, anterior to the posterior edge of the parietal scales;
5. Head width, measured at the widest part of head, posterior to the eyes.

Nomenclature follows that of Cogger (1992). Meristic values for *S. approximans*,

S. australis, *S. bimaculatus*, *S. roperi* and *S. semifasciatus* were taken from Storr (1967, 1979) and Cogger (1992).

The following abbreviations are used in the text: NTM, Museum and Art Gallery of the Northern Territory; QM, Queensland Museum; SVL, snout-vent length.

SYSTEMATICS

Simoselaps morrissi sp. nov. (Figs 1–2)

Simoselaps sp. (Photo 817) - Wilson and Knowles 1988.

Type material. HOLOTYPE – NTM R.22951, an adult male from the southern end of Eleho Island, 12°03'S 135°34'E,

Northern Territory, collected by K. Aland and A. Yumbulul, on 10 October 1996. PARATYPE -NTM R.17740, 20 km east of Goomadeer River crossing, on Maningrida road, Arnhem Land, 12°08'S 133°22'E, Northern Territory, collected by J. Woinarski, on 4 October 1992.

Diagnosis. *Simoselaps morrisi* sp. nov. is a medium sized (SVL to 268 mm), robust member of the *S. semifasciatus* subgroup, distinguished from all other *Simoselaps* by the combination of ventral plus subcaudal scale count of 159–161, six supralabials, frontal scale 1.1–1.2 times as long as wide, temporal scale arrangement 1+1+2, lower postocular scale in broad contact with anterior temporal scale, protruding snout (1.8–2.0 % of SVL), rostral tipped with sharp cutting edge, dark head blotch diffuse to virtually absent, and complete lack of dark cross-bands on the body and tail.

Description. *Head.* Head length 4.6–5.4 % of SVL. Head depth 2.2% of SVL. Head width 3.2–3.4% of SVL. Snout 1.8–2.0% of SVL, protruding beyond mouth. Rostral scale wider than high, anteriorly tipped with

sharp cutting edge and posterior apex penetrating deeply between internasal scales. Median sutures between paired internasal and prefrontal scales subequal. Frontal 1.1–1.2 times as long as wide. Nasal groove almost divides nasal scale, being a deep groove above and a complete division below nostril. Nasal scale contacting preocular scale, which is separated from frontal by single large supraocular scale. Two postocular scales, lowermost in broad contact with anterior temporal scale. Temporal scale arrangement 1+1+2. Supralabial scales six. Infralabial scales seven. Mental scale contacting first infralabial scales. Anterior chin shields contacting first three infralabial scales.

Body. Snout-vent length to 268 mm. Tail length 11.9–12.5% of SVL. Body width 3.5–3.7% of SVL. Scales smooth. Mid-body scale rows 15. Ventral scales 138–141 (mean = 140). Subcaudal scales 20–21 (mean = 20.5). Total ventral and subcaudal scales 159–161 (mean = 160). Anal and subcaudal scales divided. Tail terminating in bluntly rounded scale.



Fig. 1. Holotype of *Simoselaps morrisi* sp. nov. (NTM R.22951) from Elcho Island, Arnhem Land, Northern Territory, photographed in life. Note abraded rostral scale.

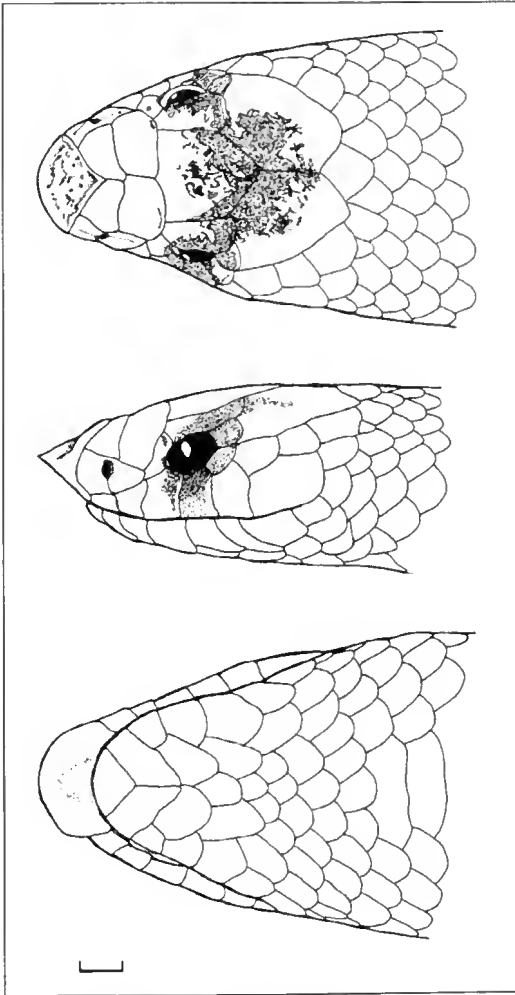


Fig. 2. Paratype of *Simoselaps morrissi* sp. nov. (NTM R.17740). Dorsal, lateral and ventral views of head scalation. Stippling indicates extent of dark head blotch. Scale bar = 1 mm.

Colour and pattern (in spirit) of holotype. *Head.* Dorsal ground colour pale, orange-brown, patterned with diffuse dark head blotch and prominent nuchal blotch. Head blotch obscure, restricted to faint blackish mottling on inner margins of parietals, posterior margins of frontal and supraoculars and inner margins of scales surrounding orbit. Nasal and anterior supralabials patterned with faint dark mottling, most pronounced on the third and fourth supralabials (suboculars). Nuchal blotch black, six vertebral scales in length, separated from posterior edge of parietals by

three vertebral scales. Anterior transverse margin of nuchal blotch sharp-edged, extending to upper edge of second last lateral scale. Posterior margin of nuchal blotch arched back on midline.

Body. Dorsal surface reddish-brown, each body scale narrowly margined with black giving the dorsum a reticulated appearance. Ventral surfaces immaculate creamy-white.

Details of holotype. (NTM R.22951) Snout-vent length 268 mm. Tail length 33.4 mm. Body width 9.26 mm. Head length 12.5 mm. Head depth 5.81 mm. Head width 8.66 mm. Frontal length 3.43 mm. Frontal width 2.92 mm. Snout length 4.73 mm. Mid-body scale rows 15. Ventral scales 138. Subcaudal scales 21. Leading edge of rostral partly abraded.

Heart and liver tissue samples were taken from the holotype at death. These are lodged in the South Australian Museum's tissue bank under the number SAM-EBU BD2.

Variation. The single paratype (NTM R.17740) is a male which, as shown in Table 1, conforms closely to the holotype in meristic and mensural characteristics. It is also very similar in colour and body pattern, differing slightly in having a more pronounced head blotch. This is extensive on the parietals, frontal and supraoculars, each being heavily mottled with dark brown on at least half of their surface (Fig. 2). The third and fourth supralabials and postoculars are also heavily blotched with dark brown. The rostral is mottled with dark brown. The specimen from Nabarlek, illustrated in Wilson and Knowles (1988: Photo 817), and a specimen from Lake Evella, photographed by Ian Morris, agree closely with the type series in colour and pattern. As other *Simoselaps* are sexually dimorphic (Clarke and How 1995), it is expected that in female *S. morrissi* the variables snout-vent length, tail length and ventral and subcaudal scale counts will differ from the type series (see Table 2).

Comparison with other species. With its shovel-shaped snout tipped with a sharp cutting edge, *S. morrissi* belongs in the *S. semifasciatus* subgroup, which comprises *S. approximans*, *S. australis*, *S. incinctus*, *S. morrissi*, *S. roperi* and *S. semifasciatus*.

Simoselaps morrisi is easily distinguished from most members of this subgroup by the absence of dark cross-bands on the body and tail. Additionally, it differs from *S. approximans*, *S. australis* and *S. semifasciatus* in having less midbody scale rows (15 vs 17), fewer ventral scales (138–141 vs 158–181, 140–170 and 147–188 respectively) and in being geographically distant. It also differs from *S. roperi* in having fewer ventral scales (138–141 vs 150–179).

Simoselaps morrisi is most similar to *S. incinctus*, the only other non-banded member of the *S. semifasciatus* subgroup. It is distinguished by having fewer total ventral and subcaudal scales (159–161 vs 166–197), by having only the lower (vs both) postocular scale in broad contact with anterior temporal scale and by being more robust (body width 3.5–3.7 vs 2.7–3.6 % of SVL; head width 3.2–3.4 vs 2.0–2.8 % of SVL). Also, in *S. morrisi* the dark head blotch is virtually absent in adults and is restricted to dense mottling in subadults. In *S. incinctus* the dark head blotch is solid and prominent in all size classes. The two species are also geographically distant (Fig. 3).

Other non-banded *Simoselaps* which could be confused with *S. morrisi* are *S. bimaculatus* and *S. warro*. *Simoselaps morrisi* differs from *S. bimaculatus* in having fewer ventral scales (138–141 vs 175–238), more supralabial scales (6 vs 5) and by not having the anterior and posterior temporal scales usually fused into a single large scale (Storr 1967); it is also geographically distant. *Simoselaps morrisi* differs from *S. warro* in having a temporal scale arrangement of 1+1+2 (vs 2+2+3), by having the nasal scale in contact with preocular scale (vs widely separated), by having a frontal scale not much longer than wide (1.1–1.2 vs 1.4–1.7 times as long as wide) and by having a more protruding snout (snout length 1.8–2.0 vs 1.4–1.8% of SVL); it is also geographically distant.

Distribution and conservation status. The known distribution of *S. morrisi* is northern Arnhem Land, Northern Territory, Australia (Fig. 3). The holotype was collected on Elcho Island and the paratype from 20 km east of the Goomadeer River. Photographic evidence also accurately places the species at Nabarlek (G. Harold, pers. comm.) and Lake Evella (I. Morris,

Table 2. Comparison of variables showing sexual dimorphism in *Simoselaps incinctus* and *S. warro*. Measurements are in mm (SD = standard deviation).

Variables	Males			Females		
	mean	SD	range	mean	SD	range
<i>Simoselaps incinctus</i>						
	n = 15			n = 6		
Snout-vent length (SVL)	252	40.6	185–324	272	40.6	234–330
Tail length	27.5	4.04	19.1–33.9	21.1	2.15	18.5–24
Tail length to SVL ratio	0.11	0.01	0.10–0.12	0.08	0.01	0.07–0.08
No. of ventral scales	161	8.84	145–175	170	4.72	164–178
No. of subcaudal scales	21.9	1.16	21–25	17.7	0.82	17–19
<i>Simoselaps warro</i>						
	n = 7			n = 2		
Snout-vent length (SVL)	271.9	29.62	218–302	318.5	9.19	312–325
Tail length	32.2	4.55	28.0–40.9	23.9	1.30	23.0–24.8
Tail length to SVL ratio	0.12	0.02	0.10–0.14	0.07	0.002	0.074–0.076
No. of ventral scales	137.0	5.38	129–143	153.0	5.66	149–157
No. of subcaudal scales	21.3	2.06	18–23	14.5	0.71	14–15

pers. comm.). The record of the species from Groote Eylandt by Wilson and Knowles (1988) is unsubstantiated.

Using the quantitative ranking method adopted by Cogger *et al.* (1993) to assess conservation status, and conservatively extrapolating some variables from congeners, *S. morrissi* is scored at 31.4. This score is within the range assigned to the 'Vulnerable' category.

Habitat and natural history. *Simoselaps morrissi* is terrestrial, semi-fossorial and nocturnal. Both type specimens were collected at night, while crossing dirt roads, in *Eucalyptus miniata* dominated woodland on sandy soil. Ian Morris's observations (pers. comm.) on several specimens at Lake Evella confirm the species preference for *E. miniata* woodland, but indicate that harder soil types may also be utilised. Both type specimens were collected in October. At capture the holotype excreted two undigested reptile egg cases.

Etymology. The new species is named for Ian James Morris, naturalist and author, in

recognition of his contribution to our understanding of the Northern Territory fauna. He first collected and photographed *S. morrissi* in 1970 at Lake Evella airstrip.

DISCUSSION

Species of *Simoselaps* are sexually dimorphic and body dimensions can be used to determine sex (Clarke and How 1995). Table 2 demonstrates this, using *S. incinctus* and *S. warro* as examples, showing that females grow to a larger size than males and that subcaudal scale counts and tail length/snout-vent length ratios can be used to determine sex. Table 2 also shows that males dominated samples by a factor much greater than 2:1. This skewed ratio may simply result from males being more active in search of mates, thereby being detected more often (Shine 1991). The majority of specimens were collected between January and May.

The literature (Storr 1967; Cogger 1992) indicates that *S. incinctus* has a constant

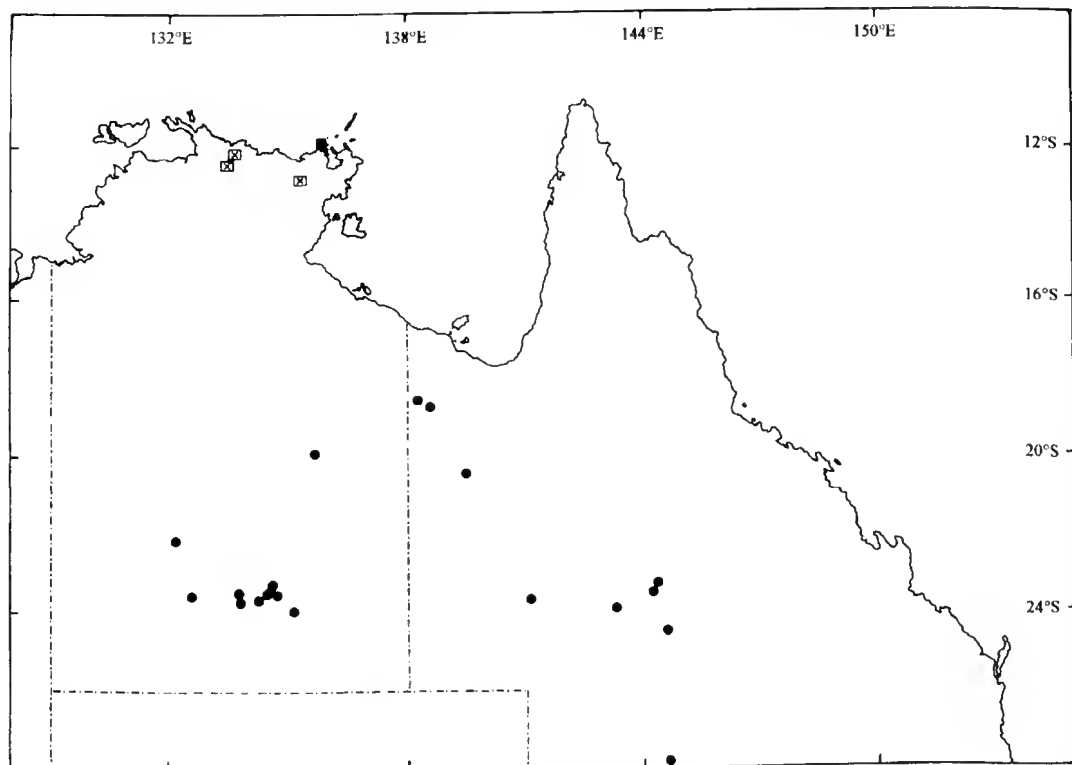


Fig. 3. Map of northern Australia showing distributions of *Simoselaps morrissi* sp. nov. (squares) and *S. incinctus* (dots). Solid square indicates type locality of *S. morrissi* sp. nov., crossed squares indicate other established localities.

count of 17 mid-body scale rows. This study shows that specimens from the eastern sector of its range in Queensland (33% of sample) (Fig. 3), consistently have 15 mid-body scale rows. As these eastern populations of *S. incinctus* are most geographically close to *S. morrisi*, character states in combination, rather than number of mid-body scale rows alone, are required to distinguish between the two species.

ACKNOWLEDGMENTS

I wish to thank Patrick Couper (QM) for allowing examination of specimens in his care. For information on *S. morrisi* habitat preferences and behaviour I am grateful to Ian Morris, Greg Harold and John Woinarski.

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APPENDIX

Comparative *Simoselaps incinctus* examined.

NORTHERN TERRITORY – Paratypes: NTM R.34168–169 (NTM2262–63), 22°08'S 132°05'E, Mount Denison Station. Non-type material: NTM R.699, 23°32'S 133°50'E, 16 km N Aliee Springs; NTM R.14332, 24°00'S 135°15'E, Ingwallum; NTM R.15599, 23°17'S 134°44'E, Red Ochre Dam; NTM R.15612, locality unknown; NTM R.18141, 19°58'S 135°41'E, Wakaya Desert; NTM R. 18236, 23°41'S 134°13'E, Corroborree Rock; NTM R.18237, NTM R.18243, 23°34'S 134°26'E, near Trephina Gorge; NTM R.18252, 23°28'S 134°43'E, Arltunga; NTM R.22701, locality unknown; NTM R.34163 (NTM119), 23°37'S 132°43'E, Ormiston Reserve; NTM R.34165 (NTM434), 23°42'S 133°53'E, Aliee Springs.

QUEENSLAND – NTM R.21461, 18°36'S 138°08'E, Stockyard Waterhole, Musselbrook Reserve; QM J.35323, 28°03'S 144°48'E, Yowah Opal Field; QM J.37943, 23°26'S 144°15'E, Longreach; QM J.39033, 20°31'S 139°26'E, 27 km W Mount Isa; QM J.41387, 23°27'S 144°15'E, Longreach area; QM J.41847, 23°46'S 141°08'E, Ooridja area, Diamantina Lakes; QM J.47968, 24°01'S 143°10'E, Stonehenge, 14 km NW Glenroy Station; QM J.52751, 18°45'S 138°35'E, Century Project Site, Lawn Hill Station; QM J.53257, 24°33'S 144°44'E, Springhill Station.

Comparative *Simoselaps warro* examined.

QUEENSLAND – NTM R.1148–49, 17°00'S 145°26'E, Mareeba; NTM R.2967, 19°34'S

147°24'E. Ayr; QM J.23333, 14°54'S 141°37'E, Edward River Community; QM J.26286, 13°56'S 143°11'E. Coen; QM J.31055, 17°00'S 145°26'E, Mareeba; QM J.40531, 13°05'S 141°57'E. Beagle Camp, via Weipa; QM J.53975, 17°00'S 145°22'E, 6 km W Mareeba; QM J.57666, 14°41'S 142°10'E, Strathgordon Homestead.

Accepted 19 November, 1997

A NEW *SEPIELLA* GRAY, 1849 (CEPHALOPODA: SEPIIDAE) FROM NORTHERN AUSTRALIA, WITH A REDESCRIPTION OF *SEPIELLA WEBERI* ADAM, 1939

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ABSTRACT

Examination of specimens of *Sepiella* Gray, 1849, from northern Australia led to the discovery of a second species in addition to *Sepiella weberi* Adam, 1939, already known to occur in the region. This species is described here as *Sepiella mangkangua* sp. nov., and *Sepiella weberi* is redescribed from the types and Australian material. The two species, while occupying a narrow geographic range, were collected at different depths. *Sepiella weberi* is found between 77–88 m in Australian waters (though the type specimens from Indonesia were collected at 18 m, and at the surface), and *S. mangkangua* sp. nov. occurs in shallow water, between 1.1 and 3.3 m.

KEYWORDS: Cephalopoda, Sepiidae, *Sepiella mangkangua* sp. nov., *Sepiella weberi*, northern Australia

INTRODUCTION

The genus *Sepiella* was erected by Gray (1849) for cuttlefish with numerous, similar sized suckers in 8–10 rows on the tentacular clubs, and with an oblong cuttlebone, convex ventrally, the posterior end of which is expanded and chitinous. The name subsequently sank into obscurity until Steenstrup (1880) later redefined the group, thus reinstating its importance (Lu 1998). Khromov *et al.* (1998) define the genus by the presence of a gland and gland pore at the posterior end of the mantle between the fins, and in having a triangular tubercle on the mantle locking cartilage which corresponds to a depression in the funnel locking cartilage. The inner cone of the sepium has very short limbs.

Khromov *et al.* (1998) recognise six species in the genus: *Sepiella cyanea* Robson, 1924; *S. inermis* d'Orbigny, 1848; *S. japonica* Sasaki, 1929; *S. ocellata* Pfeffer, 1884; *S. ornata* (Rang, 1837), and *S. weberi* Adam, 1939. The status of *S. ocellata* is described as questionable; this species is possibly a synonym of *S. ornata* (Khromov

et al. 1998). *Sepiella weberi* was the only species known from Australian waters, reported from near Darwin, 12°27'S 130°50'E (Lu 1998). It was originally described from two eastern Indonesian specimens: a male from Timor, near Koepang, 8°35'S 126°00'E, and a female from Soemba, 10°S 119°56'E. Iredale (1954) described a second species, *S. melwardi*, based on cuttlebones collected from Melville Island, Australia, 11°35'S 131°10'E. Lu (1998) placed *S. melwardi* in synonymy with *S. weberi*.

Members of this genus occur only off southern Africa, the Red Sea and the Indo-West Pacific. All species are found in relatively shallow water, with the deepest occurrence at approximately 150 m. Adam's (1939) revision of the group is the most recent detailed work on the genus. While Adam (1939) clarified the status of a number of species, it is likely that as representatives of the genus can be quite similar morphologically, a number of cryptic species may remain to be discovered.

Recent examination of all *Sepiella* material housed in the Museum of Victoria

collection led to the discovery of a new species from northern Australia. This species, the second now known to occur in Australian waters, does not conform to any of the above listed nominal species, differing in a number of characters, primarily of the cuttlebone and tentacular club. A full description of the new species is presented in this paper, with a redescription of *S. weberi*. The two species, while occupying a narrow geographic range, were collected at different depths in Australian waters. *Sepiella weberi* has been reported from between 77 and 88 m off northwestern Australia. Adam's (1939) type specimen from Soemba was collected at 18.3 m, and a second, from Timor, was collected at the surface using an electric light. *Sepiella mangkangunga* sp. nov. from Australia occurs in shallow water between 1.1 and 3.3 m.

MATERIALS AND METHODS

This work was based on museum material. All material studied is listed in the Material examined sections given with each species description. Institutional acronyms used throughout the paper are: AM – Australian Museum, Sydney, Australia; MV – Museum Victoria, Melbourne, Australia; NTM – Museum and Art Gallery of the Northern Territory; ZMA – Zoologisch Museum, Universiteit van Amsterdam. Other abbreviations: coll. – collected, F – female, FV – Fisheries Vessel, Is. – Island, J – juvenile, m – metres, M – male, mm – millimetres, RV – Research Vessel.

Measurements and indices used throughout this paper are primarily those given in Roper and Voss (1983), using dorsal mantle length (ML) as a size standard. Some additional measurements are used, and these with the definitions listed by Roper and Voss (1983) are given in Table 1. Parts of the club and arm sucker rims are described using the terminology of Nixon and Dilly (1977), and nomenclature for radulae follows Nixon (1995). Beaks were described following Clarke (1986). Diagrammatic illustrations of measurements and terminology used for particular structures are shown in Fig. 1.

Measurements were made either using dial callipers, or an eyepiece micrometer attached to a stereo microscope. All measurements are expressed in millimetres (mm). Measurements and counts for individual specimens are shown in tables accompanying descriptions. Ranges of arm length indices, arm sucker diameter indices, and arm sucker counts are also presented in tables accompanying descriptions. Ranges for all other characters appear in the text. In species descriptions and tables, the range of values for each character are expressed as: minimum – mean – maximum [standard deviation (SD)]. Values for each sex are given separately. Numbers shown in bold with the range of measurements for mantle length indicate the upper size limit for each sex (numbers appear after the upper limit of the range when the largest specimens were not necessarily among the specimens selected for detailed examination and measurement for all characters).

Measurements for structures which were clearly distorted or broken were not attempted, and these, in addition to missing values, appear as a dash (–) in the tables. Ranges for specific character traits given with each species description do not, therefore, always refer to the total number of specimens examined for each species. Measurements for *S. weberi* Adam syntypes are included in Table 4, but are not included in the ranges of indices included with species descriptions.

For scanning electron microscopy, arm and club suckers were removed from the middle of designated arms and the tentacular club, and dehydrated in an ethanol series through to 100% ethanol then air dried. Radulae and beaks were dissected from the buccal mass, and soaked for approximately half an hour in a warm, saturated potassium hydroxide solution, then radulae were cleaned using forceps and a fine brush. In all cases, the new unused portion of the radula was examined. All prepared material was mounted, gold coated and examined in a JSM 6400 (Japan Electron Optics Ltd. Japan) scanning electron microscope operated at 15 kV.

Table 1. Description of measurements and counts. Definitions largely follow Roper and Voss (1983). New or modified definitions are indicated by an asterisk (*). Indices (shown in square brackets) are calculated by dividing each measure by mantle length or, for cuttlebone characters, cuttlebone length (unless otherwise specified).

Arm Length – AL : length of each designated (i.e. 1, 2 etc.) arm measured from first basal (proximal-most) sucker to distal tip of arm (Arm 1, dorsal; 2, dorso-lateral; 3, ventro-lateral; 4, ventral) [ALI].
Anterior Mantle to Head length * – AMH : dorsal length of mantle measured from anterior-most point of mantle to intersection of transverse line joining dorso-lateral mantle margin [AMHI].
Arm Sucker Count * – ASC : total number of suckers on each designated arm (e.g. ASC2).
Arm Sucker diameter – AS : diameter of largest sucker on each designated (i.e. 1, 2 etc.) arm [ASIn]. Suckers on left ventral hectocotyliised arms are differentiated as follows:
Arm Sucker left 4 * – ASl4 : diameter of largest sucker on left ventral arm of male [ASInl4].
Arm Sucker left 4 minimum * – ASl4m : diameter of smallest arm sucker on hectocotyliised portion of left ventral arm of male [ASInl4m].
Cuttlebone Breadth – CbB : greatest dorso-ventral breadth of cuttlebone [CbBI].
Cuttlebone Length – CbL : dorsal length of cuttlebone along midline.
Cuttlebone Width – CbW : greatest width (perpendicular to longitudinal axis) of cuttlebone [CbWI].
Club Length – CL : length of tentacular club measured from proximal-most basal suckers (carpus) to distal tip of club [CLIL].
Club Row Count – CIRC : number of suckers in transverse rows (dashed line in Fig. 1) on tentacular club.
Club Sucker diameter – CIS : diameter of largest sucker on tentacular club [CISI].
Club Sucker dorsal * – CISd : diameter of largest tentacular club sucker in dorsal-most (closest to swimming keel) longitudinal row [CISId].
Club Sucker ventral * – CISv : diameter of largest tentacular club sucker in ventral-most (opposite swimming keel) longitudinal row [CISIV].
Eye Diameter – ED : diameter of eye [EDI].
Egg Diameter * – EgD : diameter of egg [EgDI].
Free Funnel length – FFu : the length of the funnel from the anterior funnel opening to the point of its dorsal attachment to the head [FFuI].
Fin Insertion anterior * – FIA : anterior origin of fin measured from mantle margin to anterior-most junction of fin and mantle [FIIa].
Fin Insertion posterior* – FIP : measured between posterior junctions of fins with mantle [FIIp].
Funnel Length – FuL : the length of the funnel from the anterior funnel opening to the posterior margin measured along the ventral midline [FuLI].
Fin Width – FW : greatest width of single fin [FWI].
Gill Lamellae Count – GiLC : number of lamellae on outer demibranch including the terminal lamella.
Gill Length * – GiL : length of gill [GiLI].
Head Length – HL : dorsal length of head measured from point of fusion of dorsal arms to anterior tip of nuchal cartilage [HLI].
Head Width – HW : greatest width of head at level of eyes [HWI].
Loculus Length * – LoL : length of the last loculus (ventral anterior smooth zone of the cuttlebone) [LoLI].
Mantle Length – ML : dorsal mantle length. Measured from anterior-most point of mantle to posterior apex of mantle.
Mantle Width – MW : greatest straight-line ventral width of mantle [MWI].
Spermatophore Length – SpL : length of spermatophore [SpLI].
Spermatophore Width – SpW : greatest width of spermatophore. Spermatophore width index is expressed as a percentage of spermatophore length [SpWI].
Striated Zone length – StZ : length of striated zone of cuttlebone [StZI].
Transverse Row Count – TrRC : number of suckers in longitudinal series on tentacular club (counted from proximal-most basal suckers (carpus) to distal tip of club).
Ventral Mantle Length – VML : length of ventral mantle measured from anterior mantle margin at ventral midline, to posterior apex of mantle [VMLI].

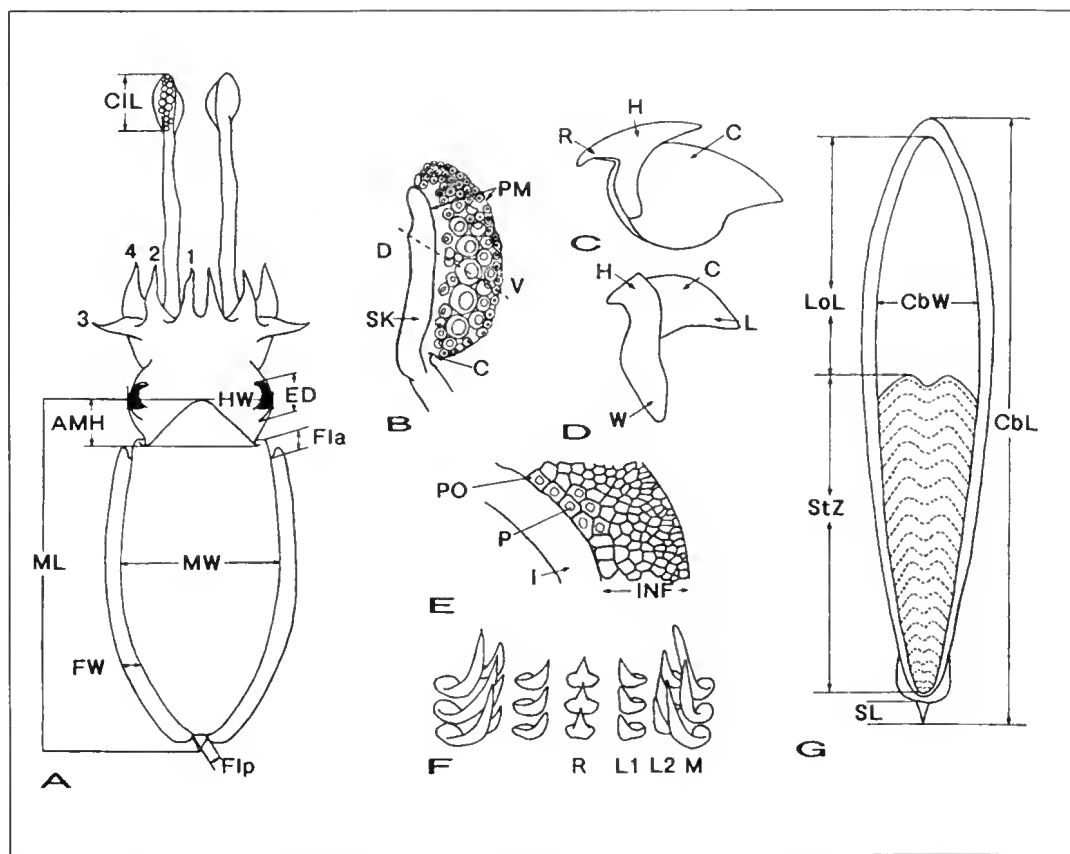


Fig. 1. Measurements and terminology. **A**, whole animal dorsal view (for abbreviations and definitions see Table 1); **B**, tentacular club (C – carpus, D – dorsal, PM – protective membranes, SK – swimming keel, V – ventral). The number of suckers intersected in an oblique transverse line across the club, shown as a hatched line on this figure, is the Club Row Count (CIRC). In the example illustrated CIRC = 4.; **C**, upper beak (C – crest, H – hood, R – rostrum); **D**, lower beak (C – crest, H – hood, L – lateral wall, W – wing); **E**, arm sucker rim (I – inner ring, INF – infundibulum, PO – polygonal process, P – peg); **F**, radula (R – rhachidian teeth, L1 – first lateral teeth, L2 – second lateral teeth, M – marginal teeth); **G**, cuttlebone, ventral view (for abbreviations and definitions, see Table 1). (A and G modified from Roper and Voss 1983: figure 1).

Species descriptions were generated by the DELTA (DEscription Language for TAXonomy) system (Dallwitz 1980; Dallwitz *et al.* 1993; Partridge *et al.* 1993).

The statistics package 'Systat' (Systat Incorporated) was used to examine sexual dimorphism in morphometric characters for *Sepiella mangkangua* sp. nov. Slopes and intercepts of regression equations were compared statistically between sexes for those characters showing a significant correlation with body size. For soft parts, mantle length was used as a size indicator. For cuttlebone characters, cuttlebone length was used. An insufficient number of male

specimens available for study precluded similar comparisons between sexes being made for *Sepiella weberi*.

SYSTEMATICS

Sepiella mangkangua sp. nov. (Figs 1-11; Tables 1-6)

Sepiella melwardi Iredale, 1954: 78–79 (in part), plate V, figs 4–6.

Type material. HOLOTYPE – NTM P10606, Australia: Northern Territory, off Stingray Head – M (42.0 mm ML), 12°48'S

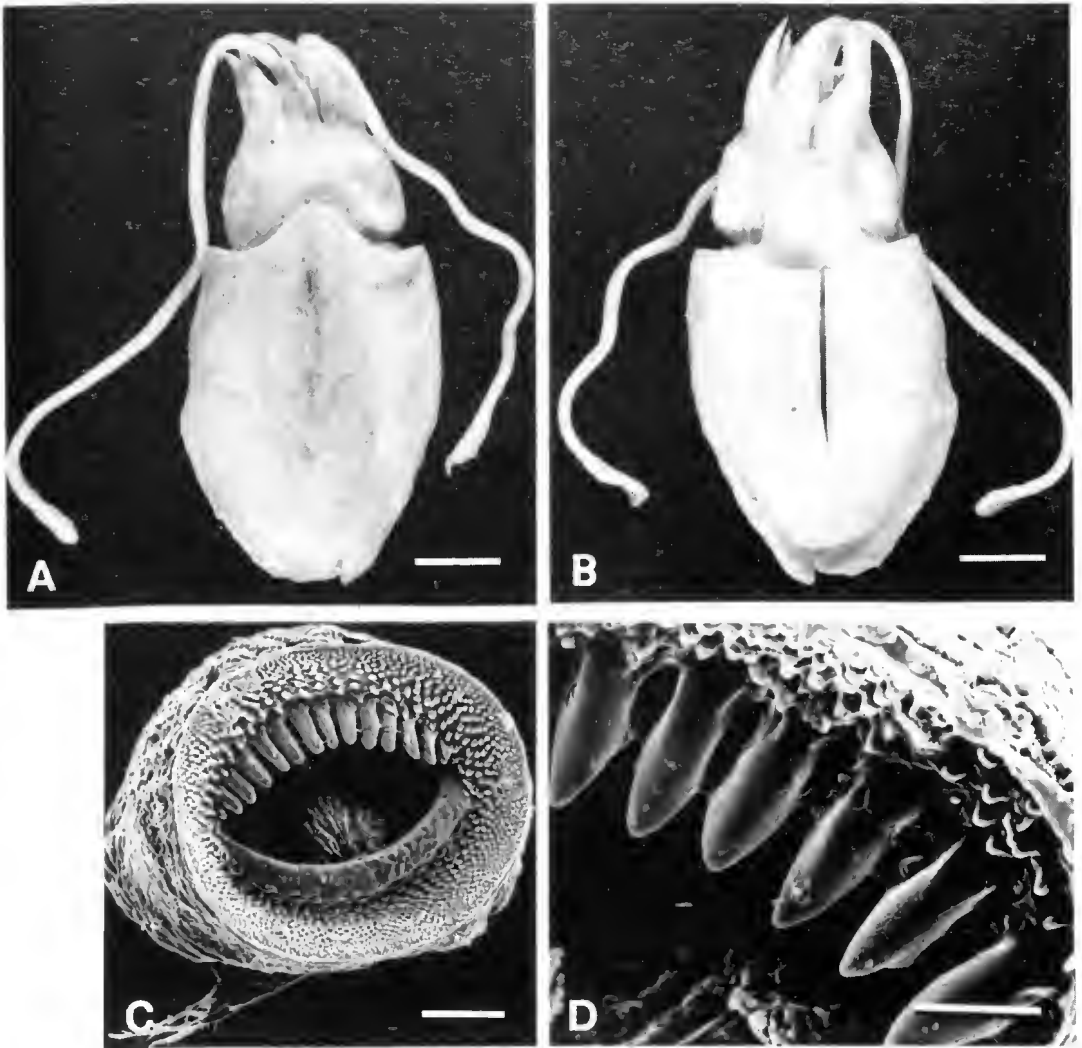


Fig. 2. *Sepiella mangkangunga* sp. nov. **A**, dorsal view, male, MV F65573, 41.5 mm ML, scale bar 10 mm; **B**, ventral view, same specimen; **C**, sucker, arm 2, male, NTM P11116, 34.0 mm ML, scale bar 100 μ m; **D**, enlargement of sucker rim arm 2, male, NTM P11116, 48.1 mm ML, scale bar 30 μ m.

130°21'E, 2.3–2.1 m, 5 June 1987, coll. N. Gill, N.T. Fisheries. PARATYPES – (NTM P16082), Australia: Northern Territory, off Stingray Head – 2M (45.7, 38.0 mm ML), 2F (43.2, 52.2 mm ML), 12°48'S 130°21'E, 2.3–2.1 m, 5 June 1987, coll. N. Gill, N.T. Fisheries; (MV F80992), collection data as for NTM P16082 – 3M (38.6–45.8 mm ML) 3F (45.2–34.7 mm ML).

Additional material. Australia: Northern Territory – 1 cuttlebone (44.0 mm CbL), Melville Is., Condon Bay, 11°35'S 131°10'E, on beach, coll. M. Ward, (AM

C133321); 14M (23.1–52.5 mm ML) 12F (24.6–57.8 mm ML) 16J (16.3–26.5 mm ML), off Stingray Head, 12°48'S 130°21'E, 2.1–1.2 m, 18 August 1987, coll. N. Gill on FV *John Lake*, (MV F65574); 10M (24.8–57.6 mm ML) 7F (23.7–57.2 mm ML) 2J (17.6, 21.2 mm ML), 2.8–1.1 m, 3 September 1987, coll. N. Gill on FV *John Lake*, (NTM P11116); 19M (32.2–50.5 mm ML) 7F (34.8–55.0 mm ML) 31J (16.1–35.0 mm ML), 2.6–1.6 m, 4 June 1987, coll. N. Gill, N.T. Fisheries, (MV F65572); 5M (37.7–41.5 mm ML) 8F (39.1–48.0 mm ML)

45J (18.2–34.9 mm ML), 2.3–2.1 m, 5 June 1987, coll. N. Gill, N.T. Fisheries, (MV F65573); 7F (36.1–54.0 mm ML) 7J (14.7–31.1 mm ML), mouth of Finnis River, 12°53'S 130°32'E, 3.3–2.5 m, 4 June 1987, coll. N. Gill, N.T. Fisheries, (MV F65569); 2M (28.7, 32.9 mm ML) 9F (24.0–58.5) 2J (19.3, 30.8 mm ML), Finnis River Channel, 12°53'S 130°32'E, 2.9–1.5 m, 5 June 1987, coll. N. Gill, N.T. Fisheries, (NTM P11117); 3M (33.3–40.1 mm ML) 3F (32.3–50.6 mm ML), Little Finnis River, 13°14'S 130°57'E, 1.2 m, 4 June 1987, coll. N.T. Fisheries, (MV F65576).

Diagnosis. Club with 12–15 suckers in transverse rows; swimming keel shorter than carpus. Dorsal mantle without ovoid markings at base of fins. Cuttlebone strongly convex in lateral view; postero-lateral margin of outer cone with pronounced indentation.

Description. Counts and indices for individual specimens are given in Tables 2–3; ranges for arm length indices, arm sucker diameter indices and arm sucker counts are shown in Table 4.

Small to moderate sized species; ML males 38.0–45.1–57.6 (SD, 6.5), females 43.2–53.4–57.7, **58.5** (SD, 4.6). Mantle oval; MWI males 45.7–57.5–67.4 (SD, 8.4), females 49.1–55.5–68.2 (SD, 7.0); dorsal anterior margin triangular, obtuse (Fig. 2A); extending anteriorly to level of middle of eyes; AMHI males 9.7–11.9–13.8 (SD, 1.5), females 8.0–10.9–13.0 (SD, 1.6). Ventral mantle margin emarginate, without distinct lateral angle (Fig. 2B); VMLI males 66.0–78.3–84.1 (SD, 5.1), females 75.8–80.9–85.9 (SD, 3.6). Fins widest in posterior third; FWI males 15.7–18.3–20.0 (SD, 1.3), females 16.7–19.0–21.3 (SD, 1.8); anterior origin posterior to mantle margin; FIIa males 6.0–11.0–15.8 (SD, 3.3), females 4.7–9.4–14.4 (SD, 3.6); ending in lobes which lie very close together; narrow gap between fins; FIIP males 2.4–3.3–4.1 (SD, 0.7), females 1.6–2.2–2.9 (SD, 0.5). Funnel long, broad-based; extends to interbrachial area of ventral arms (Fig. 2B); FuLI males 25.7–35.2–42.2 (SD, 5.2), females 28.3–33.9–40.2 (SD, 4.2). Funnel free portion approximately half funnel length; FFuI males 10.4–14.9–20.4 (SD, 3.2),

females 11.0–15.5–20.5 (SD, 2.8). Funnel organ dorsal elements inverted V-shape with small papilla in front; ventral elements oval (Fig. 3A). Mantle-locking cartilage curved, with triangular tubercle; funnel-locking cartilage with depression which corresponds to tubercle (Fig. 3B). Head short; HLI males 27.6–33.6–38.1 (SD, 3.5), females 28–33.8–41.2 (SD, 4.6); broad, narrower than mantle; HWI males 43.7–47.9–53.2 (SD, 2.9), females 40.1–47.5–52.6 (SD, 4.8). Eyes moderate size; EDI males 13.0–15.5–19.5 (SD, 1.9), females 13.0–15.8–17.6 (SD, 1.6); ventral eyelids present.

Male and female arms subequal in length (Table 4). Arm length index of longest arms in males (AL14) 50.4–60.5–73.5 (SD, 7.3), females (AL14) 34.7–44.3–57.5 (SD, 8.9). Protective membranes in both sexes narrow; normal, not thickened. Distal arm tips in both sexes strongly attenuate, suckers enclosed by protective membranes. Arm suckers tetraserial in both sexes. Two median series of suckers larger than dorsal and ventral marginal series in males; larger than female arm suckers (Fig. 11, Tables 4–5). Chitinous rims of arm suckers with marked sexual dimorphism. In males, distal margin of inner ring with 14–16 elongate tooth-like processes (Fig. 2C–D), proximal margin smooth; in females, distal half of inner ring with two to three rows of tooth-like structures, inner ring proximal margin with blunt projections (Fig. 4A); infundibulum in both sexes with 11–15 rows of hexagonal processes with pegs on innermost rows, outer processes without pegs (Figs 2C, 4A). In males, infundibular processes on inner margin of toothed side of ring narrow, elongate (Fig. 2C–D). Sucker counts range from 60–130; females with higher average counts than males (Table 4).

Hectocotylus present in males, left ventral arm modified; sucker size reduced proximally, eight to nine rows of reduced suckers; suckers in two dorsal series smaller than remaining suckers (Fig. 3C); two dorsal series widely spaced, suckers markedly reduced; two ventral series close together, suckers alternate; maximum and minimum sucker diameters: ASIn14 2.47–2.69–2.98 (SD, 0.13), ASIn14m 0.30–0.55–0.71 (SD, 0.12). Oral surface of

Table 2. Measurements (mm), counts and indices of 10 male *Sepiella mangkangunga* sp. nov.

Museum Reg. No.	NTM P16082 (Paratype)	MV F80992 (Paratype)	MV F80992 (Paratype)	MV F65573 (Paratype)	NTM P10606 (Holotype)	NTM P16082 (Paratype)	MV F80992 (Paratype)	MV F65574 (Paratype)	MV F65574 (Paratype)	NTM P11116 (Paratype)
Maturity	immature	immature	immature	immature	mature	mature	mature	mature	mature	mature
ML	38.0	38.6	39.3	41.5	42.0	45.7	45.8	49.6	52.5	57.6
AMHI	11.6	11.4	13.7	13.3	13.8	9.8	11.6	13.1	9.7	11.1
VMLI	81.8	77.2	76.1	66.0	78.8	76.8	84.1	80.0	83.4	79.2
MWI	62.4	65.3	67.4	65.8	61.4	55.4	57.4	47.6	45.7	46.2
FWI	18.4	17.4	18.1	15.7	17.4	18.2	18.8	19.0	20.0	19.8
AFII	15.8	12.2	11.5	14.5	11.9	9.8	13.8	6.0	8.4	6.3
PFII	3.9	3.1	2.5	4.1	2.4	3.5	3.3	-	-	-
FuLI	42.1	38.9	33.1	42.2	32.1	37.2	37.1	32.3	25.7	31.3
FFuI	15.8	16.8	20.4	12.0	16.7	17.5	15.3	12.1	11.6	10.4
HLI	37.9	35.0	34.4	38.1	35.7	27.8	33.6	32.5	32.8	27.6
HWI	53.2	47.9	47.1	47.7	46.2	45.5	43.7	49.6	51.8	46.7
EDI	19.5	14.8	15.3	13.3	14.3	16.8	15.5	15.5	16.8	13.0
AL1I	43.4	46.6	44.5	62.7	53.6	48.1	54.6	40.3	43.8	36.5
AL2I	52.6	47.9	44.5	50.6	56.0	48.1	54.6	46.4	47.6	39.9
AL3I	52.6	49.2	53.4	62.7	61.9	55.8	65.5	52.4	53.3	46.9
AL4rI	60.5	62.2	56.0	73.5	64.3	56.9	67.7	50.4	53.3	-
AL4lI	60.5	62.2	58.5	66.3	64.3	52.5	72.1	54.4	57.1	53.8
AS1In	2.29	3.24	2.54	3.25	2.98	2.89	2.73	2.62	2.99	2.52
AS2In	2.50	2.90	2.54	2.89	2.98	2.74	2.62	2.52	2.99	2.60
AS3In	2.37	2.59	2.42	2.70	3.10	2.74	2.62	2.62	2.70	2.52
AS4rIn	2.63	2.85	2.54	2.58	2.55	2.74	2.73	2.62	2.70	2.08
ASC1	60	66	74	70	75	72	74	64	76	65
ASC2	64	76	72	74	76	74	78	69	82	68
ASC3	84	90	96	98	94	84	88	82	94	90
ASC4	78	90	85	90	88	94	92	84	86	80
AS41In	2.63	2.59	2.47	2.65	2.98	2.74	2.73	2.76	2.70	2.60
AS41mln	0.18	0.18	0.18	0.17	0.17	0.22	0.15	0.14	0.29	-
CILI	34.2	46.6	38.2	37.3	40.5	35.0	32.8	-	-	36.5
CIRC	12	12	14	12	12	14	14	-	-	15
TrRC	50	60	52	42	45	55	43	-	-	52
CISI	0.58	0.65	0.64	0.60	0.60	0.55	0.55	-	-	0.69
CISdI	0.45	0.57	0.43	0.53	0.48	0.48	0.55	-	-	0.61
CISvI	0.45	0.52	0.51	0.48	0.48	0.55	0.55	-	-	0.64
GiLC	25	25	26	-	-	25	26	26	25	26
GiLI	36.8	36.8	36.4	31.6	41.9	34.8	37.3	25.0	26.9	26.2
SpLI	-	-	-	-	7.8	7.6	8.5	8.5	8.6	8.7
SpWI	-	-	-	-	0.24	0.26	0.26	0.24	0.23	0.26
CbL	36.0	36.8	36.5	39.9	42.4	44.3	47.0	47.0	47.7	-
CbWI	30.6	30.7	30.7	32.1	33.0	30.2	27.4	29.1	31.4	-
CbBI	15.3	15.5	15.1	15.0	14.4	15.8	14.5	11.9	14.5	-
StZI	48.6	48.9	54.8	50.1	50.8	54.2	49.7	55.3	56.0	-
LoLI	40.3	38.0	38.4	40.1	40.6	37.7	38.4	31.9	28.5	-
LoLSz(%)	82.9	77.8	70.0	80.0	80.0	69.6	77.3	57.7	50.9	-

Table 3. Measurements (mm), counts and indices of 10 female *Sepiella mangkungunga* sp. nov.

Museum Reg. No.	NTM P16082 (Paratype)	MV F65574 (Paratype)	MV F80992 (Paratype)	NTM P16082 (Paratype)	NTM P11116 (Paratype)	MV F80992 (Paratype)	MV F65574 (Paratype)	NTM P11116	NTM P11117	MV F65574
Maturity	immature	immature	immature	immature	mature	mature	mature	mature	mature	mature
ML	43.2	48.9	51.2	52.2	54.6	54.7	56.8	57.2	57.4	57.7
AMH1	13.0	12.1	12.3	9.0	9.7	11.2	10.2	8.0	10.6	12.5
VML1	75.9	83.2	75.8	78.9	85.9	77.5	84.9	83.2	81.7	81.6
MWI	66.7	49.1	58.2	68.2	52.7	55.0	51.8	49.1	54.7	49.2
FWI	16.7	19.0	21.3	17.2	20.0	21.0	21.0	18.7	17.2	18.2
AFII	12.0	4.7	12.5	12.8	5.5	14.4	8.1	5.8	11.5	6.8
PFII	1.6	-	2.0	2.9	-	2.4	-	-	-	-
FuLI	39.4	30.7	28.3	40.2	34.8	36.6	29.9	33.2	36.6	29.5
FFul	18.5	14.3	20.5	15.3	11.0	17.4	15.8	13.1	14.8	13.9
HLI	38.0	29.7	41.2	37.4	32.4	35.6	28.2	28.1	37.1	30.3
HWI	50.0	52.1	41.0	47.5	52.6	41.7	50.2	50.9	40.1	49.0
EDI	16.4	16.2	13.9	16.1	13.0	16.8	17.6	14.3	16.2	17.5
AL1I	38.2	28.6	46.9	45.0	36.6	40.2	33.5	29.7	48.8	31.2
AL2I	41.7	34.8	46.9	47.9	39.4	40.2	29.9	33.2	48.8	34.7
AL3I	44.0	36.8	50.8	46.0	38.5	42.0	33.5	36.7	50.5	34.7
AL4I	52.1	34.8	52.7	52.7	38.5	46.6	38.7	35.0	57.5	34.7
AS1In	1.62	0.92	1.56	1.53	1.59	1.37	1.76	1.75	1.34	2.08
AS2In	1.74	1.23	1.46	1.53	1.74	1.59	1.76	1.84	1.31	1.73
AS3In	1.74	1.57	1.56	1.48	1.59	1.59	1.62	1.75	1.31	1.39
AS4In	1.44	1.43	1.46	1.44	1.83	1.37	1.76	1.84	1.39	1.73
ASC1	88	108	100	96	98	96	-	98	94	102
ASC2	98	112	116	120	-	98	-	114	110	104
ASC3	112	118	130	120	-	104	-	120	120	108
ASC4	90	114	126	118	100	110	112	108	106	100
CILI	41.7	-	41.0	38.3	45.8	35.6	37.0	-	34.8	-
CIRC	14	-	15	14	15	15	15	-	15	-
TrRC	50	-	50	54	52	48	54	-	54	-
CISI	0.58	-	0.49	0.48	0.77	0.46	0.70	-	0.44	-
CISdI	0.46	-	0.39	0.38	0.59	0.46	0.48	-	0.44	-
CISvI	0.46	-	0.39	0.42	0.73	0.46	0.79	-	0.44	-
GiLC	26	28	26	26	28	25	30	28	28	30
GiLI	39.6	31.5	35.9	46.2	27.5	37.5	29.6	26.9	37.6	22.2
EgLI	-	-	-	-	5.2	-	3.9	4.5	2.8	4.7
CbL	42.7	46.0	50.5	49.6	-	49.4	57.0	55.0	54.4	55.0
CbWI	23.2	33.5	30.7	33.1	-	33.4	31.1	30.6	32.7	32.7
CbBI	14.0	15.9	13.7	15.9	-	15.4	14.9	14.4	14.7	14.9
StZI	49.2	50.4	48.5	50.4	-	44.5	52.6	50.5	53.3	47.3
LoLI	39.8	36.7	41.6	39.3	-	44.5	33.3	34.2	36.8	38.2
LoLStz(%)	81.0	72.8	85.7	78.0	-	100.0	63.3	67.9	69.0	80.8

modified region wide, fleshy, with transversely grooved ridges; without distinct median furrow (Fig. 3C). Hectocotylised arm not markedly attenuate distally.

Tentacular club similar length in males and females; CILI males 32.8–37.6–46.6

(SD, 4.4), females 34.8–39.2–45.8 (SD, 3.9). Club crescent-shaped; sucker-bearing face convex. Club with 12–15 suckers in transverse rows, CIRC males 12–15, females 14–15; 42–60 suckers in longitudinal series, TrRC males 42–50–60 (SD, 6), females

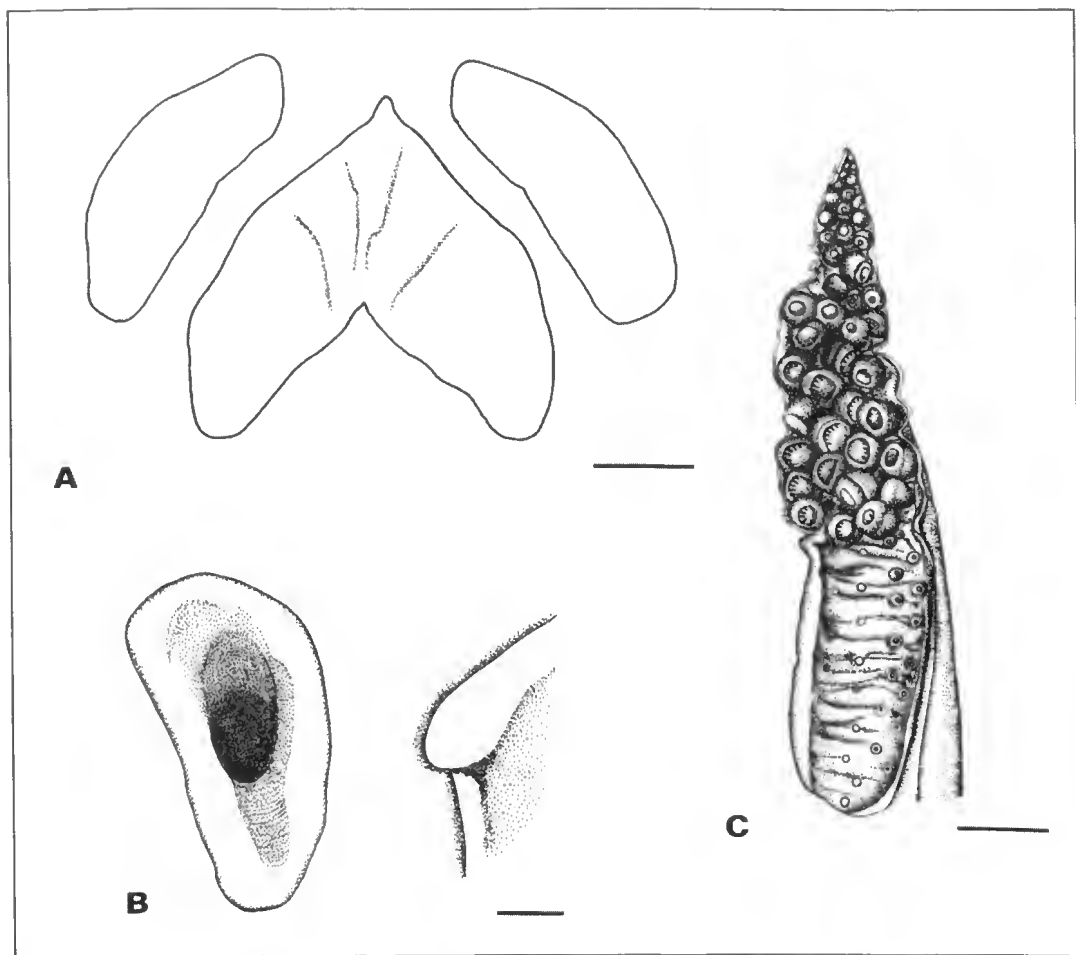


Fig. 3. *Sepiella mangkangunga* sp. nov.: A, funnel organ, male, NTM P11116, 37.3 mm ML, scale bar 2 mm; B, funnel locking cartilage (left), and mantle locking cartilage (right), female, MV F65576, 44.8 mm ML, scale bar 1 mm; C, hectocotylus, male, MV F65574, 52.5 mm ML, scale bar 3 mm.

48–52–54 (SD, 2). Suckers all similar size, minute (Fig. 5); CISI males 0.55–0.61–0.69 (SD, 0.05), females 0.44–0.56–0.77 (SD, 0.13); dorsal and ventral marginal longitudinal series of suckers similar in size; CISId males 0.43–0.51–0.61 (SD, 0.06), females 0.38–0.46–0.59 (SD, 0.07); CISlv males 0.45–0.52–0.64 (SD, 0.06), females 0.39–0.53–0.79 (SD, 0.16). Sucker dentition: half inner ring circumference in both sexes with elongate, rectangular teeth (Fig. 4D), remaining half with blunt projections; infundibulum with approximately 7–10 hexagonal processes with elongate pegs (Fig. 4B–D); at periphery, processes smaller, flattened, without pegs (Fig. 4C, D). Swimming keel of club shorter than

carpus (Fig. 5). Dorsal and ventral protective membranes not fused at base of club; joined to stalk; dorsal and ventral membranes same length, extend beyond carpus along stalk; dorsal membrane forms shallow cleft at junction with stalk.

Gills with 25–30 lamellae per demibranch; GiLC males 25–25–26 (SD, 0.5), females 25–27–30 (SD, 2). Gill length: GiLI males 25.0–33.4–41.9 (SD, 5.7), females 22.2–33.4–46.2 (SD, 7.2).

Buccal membrane without suckers. Upper beak (Fig. 6A) rostrum sharply pointed, long, curved, length greater than width, cutting edge straight; hood high above crest posteriorly; wings and hood narrow, short;

Table 4. *Sepiella mangkangunga* sp. nov.; ranges of arm length indices (ALI), arm sucker diameter indices (ASIn) and arm sucker counts (ASC) of 10 mature males and 10 mature females. min. = minimum, max. = maximum, SD = standard deviation.

	Males				Females			
	min.	mean	max.	SD	min.	mean	max.	SD
ALI1	36.5	<u>47.4</u>	62.7	7.7	28.6	<u>37.9</u>	48.8	7.3
ALI2	39.9	<u>48.8</u>	56.0	4.8	29.9	<u>39.7</u>	48.8	6.6
ALI3	46.9	<u>55.4</u>	65.5	6.1	33.5	<u>41.3</u>	50.8	6.3
ALI4	50.4	<u>60.5</u>	73.5	7.3	34.7	<u>44.3</u>	57.5	8.9
ASIn1	2.29	<u>2.80</u>	3.25	0.32	0.92	<u>1.55</u>	2.08	0.31
ASIn2	2.50	<u>2.73</u>	2.99	0.20	1.23	<u>1.59</u>	1.84	0.21
ASIn3	2.37	<u>2.64</u>	3.10	0.20	1.31	<u>1.56</u>	1.75	0.14
ASIn4	2.08	<u>2.60</u>	2.85	0.21	1.37	<u>1.57</u>	1.84	0.19
ASC1	60	<u>70</u>	76	5	88	<u>98</u>	108	5
ASC2	64	<u>73</u>	82	5	98	<u>109</u>	120	8
ASC3	82	<u>90</u>	98	5	104	<u>116</u>	130	8
ASC4	78	<u>87</u>	94	5	90	<u>108</u>	126	10

jaw angle approximately 90°; hood dark brown, fading toward lateral ventral margin, crest dark brown medially, paler brown laterally. Lower beak (Fig. 6B–C) rostral edge curved; rostrum protruding only slightly; hood low on crest; crest straight; no indentation on lateral wall edge; hood and wings width narrow; hood notch absent; wings widely spaced; crest wide; rostrum pigmented dark brown, fading on wings, crest pigmented, darkest medially. Radula homodont; rhachidian teeth with truncate bases, blunt, triangular, sides straight (Fig. 4E–F); first lateral teeth slightly longer than rhachidian teeth, broader with wide heels, asymmetrical with mesocone displaced toward centre of radula (Fig. 4E–F); second laterals longer than first, curved with broad heels; marginal teeth elongate, tapering, curved (Fig. 4E). Digestive tract: (Fig. 6D) paired salivary glands approximately 1/4 length of buccal mass; paired digestive glands large, located close together, with triangular lobes posteriorly, ducts (not shown in Fig. 6) connect digestive glands near midline with caecum, ducts with branched attached pancreatic tissue; oesophagus running dorsally along median junction of digestive glands, joining sac-like stomach immediately posterior to digestive glands; caecum disc-like, grooved in blunt V-shape anteriorly, surface lining finely pleated; intestine undifferentiated; ink sac and anal flaps well developed.

Male reproductive tract: testis on left posterior side of viscero-pericardial coelom; at distal end, convoluted vas deferens opening into broad, cone-shaped mucilaginous gland, then narrower, curved, spermatophoric gland (Fig. 7A). Close to junction with lobe-shaped accessory gland and gland appendix, delicate ciliated canal joining spermatophoric gland; distal deferent canal connects appendix of accessory gland to spermatophoric sac; genital orifice opening dorsal to left gill in anterior end of mantle cavity. Spermatophores: cement body bipartite (Figs 7B, 8A–B); aboral end cylindrical, tapering toward oral end, connecting to sperm reservoir via narrow duct extending from nipple-like tip of cement body, connects to oral end by distinct fold; oral end narrower than aboral end, tapering; ejaculatory apparatus coiled, extending into oral dilation of spermatophore. Spermatophores 3.3–5.0 mm long (SD, 0.58), 0.10–0.15 mm wide (SD, 0.01); SpLI 7.6–8.3–8.7 (SD, 0.4); SpWI 0.23–0.25–0.26 (SD, 0.01).

Female reproductive tract: ovary hangs from dorsal wall of posterior viscero-pericardial coelom. Oviduct thin-walled, continuous with body cavity; distally with thickened, glandular walls (oviducal glands). Nidamental glands in mature animals occupy large portion of ventral side of mantle cavity. Accessory nidamental glands

Table 5. Morphological parameters showing sexual dimorphism in *Sepiella mangangkunga* sp. nov. Regression data relating to Figure 11 where $Y = a + bX$ where Y = dependent variable, a = intercept, b = slope, X = ML. Sig. = significant difference between the regression lines of males (M) and females (F) with respect to intercept, N = number of specimens. r^2 proportion of total variation accounted for by regression.

Y	Sex	N	r^2	a	b	Sig.
AL3	M	10	0.477	7.53	0.384	$P < 0.01$
	F	10	0.086	10.20	0.221	
AS1	M	10	0.572	0.20	0.023	$P < 0.001$
	F	10	0.446	-0.72	0.029	
AS2	M	10	0.792	0.04	0.026	$P < 0.001$
	F	10	0.452	-0.27	0.021	
AS4	M	10	0.580	0.43	0.016	$P < 0.001$
	F	10	0.630	-0.57	0.026	
CbW	M	9	0.878	2.17	0.240	$P < 0.001$
	F	8	0.881	1.33	0.283	
StZ	M	9	0.909	-7.03	0.693	$P < 0.001$
	F	9	0.819	-4.84	0.592	

anterior to nidamental glands (Fig. 7C). Eggs spherical, 1.6–2.8 mm diameter (SD, 0.4); EgDI 2.8–4.2–5.2 (SD, 0.8).

Subdermal cartilaginous layer between cuttlebone and skin absent. Cuttlebone length approximately equal to mantle length; outline oblong, widest medially, tapers toward either end (Fig. 9A–B); CbL males 36.0–41.1–47.7 (SD, 4.5), females 42.7–51.1–57.0 (SD, 4.8); CbW1 males 29.1–30.8–33.0 (SD, 1.3), females 23.2–31.2–33.5 (SD, 3.2); strongly convex in lateral view (Fig. 9C); CbB1 males 11.9–14.7–15.8 (SD, 1.1), females 13.7–14.8–15.9 (SD, 0.9). Bone bluntly rounded anteriorly and posteriorly; strongly recurved ventrally. Dorsal surface creamy white; evenly convex; texture smooth, not pustulose. Dorsal median rib present, distinct, broadening anteriorly; lateral ribs absent. Chitin surrounding entire margin of cuttlebone. Spine absent. Striated zone convex; StZ1 males 48.6–52.0–56.0 (SD, 3.0), females 44.5–49.6–53.3 (SD, 2.7). Last loculus convex; LoL1 males 28.5–37.1–40.6 (SD, 4.1), females 33.3–38.3–44.5 (SD, 3.5); approximately 2/3 length of striated zone at midline, LoL/StZ(%) males 50.9–71.8–82.9 (SD, 11.0), females 63.3–77.6–100.0 (SD,

11.1); loculus extending posteriorly as narrow margin on each side of striated zone. Suleus extending along side of striated zone only; shallow, wide; flanked by rounded ribs. Last loculus with pronounced median indentation. Anterior striae inverted U-shape, slightly wavy (Fig. 9B). Limbs of inner cone short, extend anteriorly to junction of striated zone and posterior termination of last loculus. Inner cone limbs narrow anteriorly, broaden slightly posteriorly; thickened; not raised to form ledge posteriorly (Fig. 9D). Outer cone chitinous, spatulate, expanded; narrow anteriorly, broadening posteriorly; posterio-lateral wall with pronounced indentation in males and slight indentation in females; limbs expanded, extending posteriorly beyond inner cone, recurved ventrally (Fig. 9C–D).

Papillae absent. Colour (alcohol preserved specimens): head and arms with few scattered chromatophores (Fig. 2A); dorsal mantle pale, peppered with scattered purple-black chromatophores; paired dorsal eye spots absent. Fins pale; without markings at base. Ventral pigment absent (Fig. 2B).

Distribution. Australia: Northern Territory, 12°48'S 130°21'E to 13°14'S 130°57'E (Fig. 10). Bones collected from Melville Is., Condon Bay, 11°35'S 131°10'E. Depth range 1.1–3.3 m. Habitat sand.

Remarks. The modification of the hectocotylus in *Sepiella mangangkunga* sp. nov. is clearly visible in all males examined here, including those deemed to be immature due to the absence of fully developed spermatophores in the spermatophoric sac. In addition to the secondary sexual modification of the hectocotylus described above, there are a number of statistically significant morphometric differences between the sexes (Fig. 11). Regression data relating to the features shown in this Figure are given in Table 5. With respect to mantle length, the length of the third arm and the diameters of the first, second and fourth arm suckers tend to be greater in males than females. With respect to cuttlebone length, the width of the cuttlebone is greater in females than in males and the length of the striated zone is greater in males than females (Fig. 11). *Sepiella mangangkunga* sp. nov.

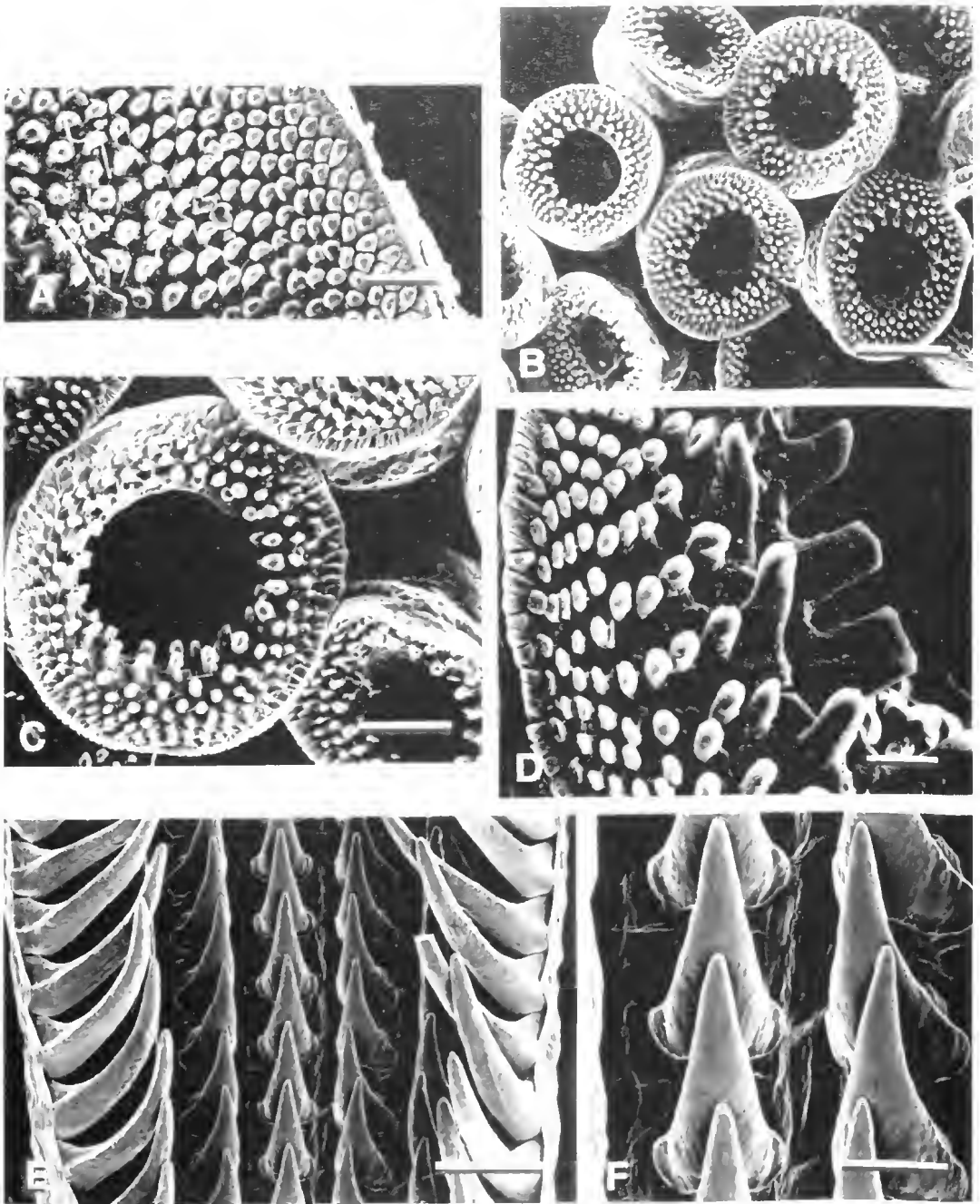


Fig. 4. *Sepiella mangkangunga* sp. nov.: A, sucker rim, arm 4, female, NTM P11116, 55.5 mm ML, scale bar 30 µm; B, club suckers, male, NTM P11116, 34.0 mm ML, scale bar 100 µm; C, enlargement of club sucker, same specimen, scale bar 50 µm; D, club sucker rim, female, NTM P11116, 55.5 mm ML, scale bar 20 µm; E, radula, female, NTM P11116, 57.2 mm ML, scale bar 200 µm; F, enlargement of rhachidian (left) and first lateral teeth (right), same specimen, scale bar 100 µm.

differs from *S. weberi* Adam in a number of characters. *Sepiella mangkangunga* sp. nov. has a greater number of club suckers in the

transverse rows (CIRC 12–15) than *S. weberi* (CIRC 7–10). The club swimming keel in *S. mangkangunga* sp. nov. is shorter

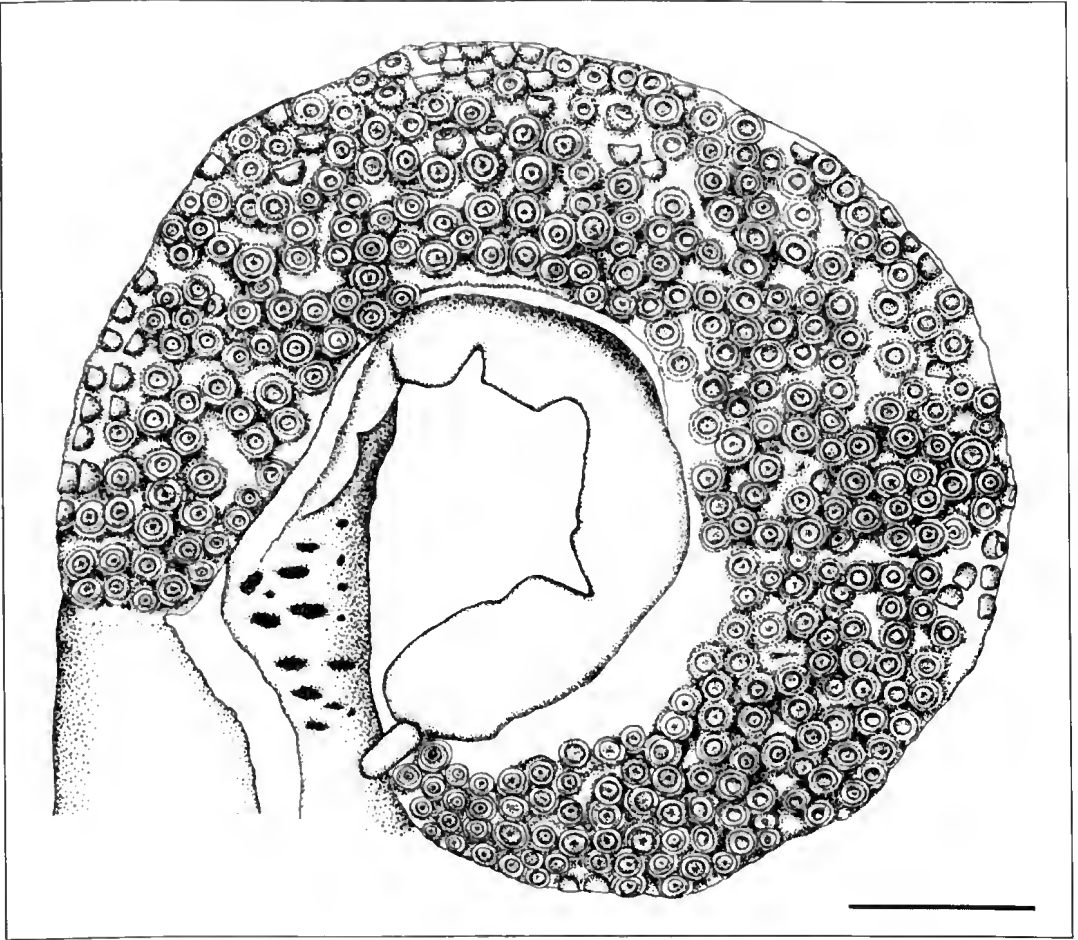


Fig. 5. *Sepiella mangkangunga* sp. nov.: tentacular club, female, NTM P11116, 54.6 mm ML, scale bar 2 mm.

than the carpus, but is the same length as the carpus in *S. weberi*. The hood notch of the lower beak is much deeper in *S. mangkangunga* sp. nov. than in *S. weberi*. The cuttlebone of *S. mangkangunga* sp. nov. is broader (dorso-ventrally), and wider (perpendicular to the longitudinal axis of the cuttlebone) than the *S. weberi* cuttlebone, with a pronounced indentation in the postero-lateral edge of the outer cone. If an indentation is present at all in the outer cone, it is not very pronounced in *S. weberi* (compare Figs 9 and 19). The depression in the last loculus is more pronounced in *S. mangkangunga* sp. nov. than in *S. weberi*. The inner cone is thicker in *S. mangkangunga* sp. nov. than in *S. weberi* (Figs 9D and 19D), though this difference may be difficult to detect in small specimens. In addition, the

distinctive ovoid spots along the base of the fins in *S. weberi* are not seen in *S. mangkangunga* sp. nov. The latter species is found in shallow water (1.1–3.3 m), while *S. weberi* occurs at depths of 77–88 m in Australian waters (though it has been collected in shallower water elsewhere). Some differences between *S. mangkangunga* sp. nov. and other nominal species in the genus are summarised in Table 6. *Sepiella mangkangunga* sp. nov., with *S. japonica* Sasaki, 1929, differs from other nominal *Sepiella* in the absence of ovoid spots at the base of the fins. *Sepiella japonica* however, has white spots on the mantle and a whitish line along the fin bases (though these may be indistinct in preserved specimens), unlike *Sepiella mangkangunga* sp. nov., and a greater number of suckers in transverse rows

on the club (Table 6). *Sepiella mangkangunga* sp. nov. occurs in close geographic proximity to Melville Island, the type locality of *S. melwardi* Iredale, 1954 (Fig. 11). *Sepiella melwardi* was described from cuttlebones collected on the island, but was subsequently synonymised by Lu (1998) with *S. weberi*. Iredale (1954) noted that the cuttlebones collected on Melville Island were clearly separable into two morphological types. Iredale (1954) attributed these differences to sexual dimorphism and designated one, from a supposed female, as the name-bearing type. The second specimen (AM C133321), described by Iredale (1954) as a male *S. melwardi*, is in fact *S. mangkangunga* sp. nov.

Etymology. The specific name, *mangkangunga*, is a Murrinh-Patha Aboriginal word used for cuttlefish (Walsh 1994). Murrinh-Patha is spoken by the population of Wadeye located on the western coast of the Northern Territory. Gender feminine.

Sepiella weberi Adam, 1939

(Figs 12–19; Tables 6–8)

Sepiella weberi Adam, 1939: 98 – 101, plate IV, figs 1–2; text figs 6–8.

Sepiella melwardi Iredale, 1954: 78–79 (in part), plate V, figs 1–3.

Type material. SYNTYPES – (ZMA Moll. 3.39.001), Soemba - F (69.3 mm ML), 10°S 119°56'E, 18.3 m (10 fathoms), 19 February 1909, coll. Siboga Expedition; (ZMA Moll.2.39.002), Timor, off Kupang, M (59.7 mm ML); 8°35'S 126°00'E, surface (attracted to lamplight), 22 January 1909, coll. Siboga Expedition.

Additional material. Australia: Northern Territory – 1 cuttlebone (53.0 mm CbL), Melville Is., Condon Bay, 11°35'S 131°10'E, on beach, coll. M. Ward, (AM C133320) (holotype of *S. melwardi*); Western Australia – 6F (47.1–58.0 mm ML), 12°39'S 127°03'E – 12°39'S 127°06'E, 88 m, 25 March 1981, coll. RV *Hai-Kung*, (MV F65575); 1M (56.8 mm ML), North West

Shelf, 12°40'S 12°12'E – 12°40'S 127°09'E, 88–86 m, 25 February 1981, coll. C.C. Lu on RV *Hai Kung*, (MV F65571); 1M (44.5 mm ML), (MV F65579); 7F (47.0–57.8 mm ML), (MV 71713); 1F (52.0 mm ML) 19°35'S 117°12'E – 19°35'S 117°14'E, 79–77 m, 10 March 1981, coll. M.F. Gomon on RV *Hai-Kung*, (MV F65577).

Diagnosis. Club with 7–10 suckers in transverse rows; swimming keel, and club protective membranes terminate at level of carpus. Dorsal mantle with five to six ovoid spots at base of each fin in both sexes. Cuttlebone not strongly convex in lateral view; postero-lateral margin of outer cone without pronounced indentation.

Description. Counts and indices for individual specimens are given in Table 7; ranges for arm length indices, arm sucker diameter indices and arm sucker counts are shown in Table 8.

Small to moderate sized species; ML males 44.5–50.7–56.8 **59.7** (SD, 8.7), females 48.0–52.2–58.0 **69.3** (SD, 3.5). Mantle oblong: MWI males 52.8–54.5–56.2 (SD, 2.4), females 45.0–51.5–55.2 (SD, 4.1); dorsal anterior margin triangular, obtuse; extending anteriorly to level of middle of eyes (Fig. 12A); AMHI males 11.5–11.9–12.3 (SD, 0.6), females 8.7–10.6–12.9 (SD, 1.7). Ventral mantle margin emarginate, without distinct lateral angle (Fig. 12B); VMLI males 82.5–84.0–85.6 (SD, 2.2), females 80.2–84.0–85.8 (SD, 2.2). Fins widest in posterior third: FWI males 10.3–11.4–12.5 (SD, 1.5), females 10.0–12.6–15.8 (SD, 2.2); anterior origin posterior to mantle margin; FIIa males 11.4–12.5–13.5 (SD, 1.4), females 9.8–12.9–16.9 (SD, 2.8); ending in lobes which lie very close together; narrow gap between fins: FIIP males 4.5, females 2.0–3.8–4.6 (SD, 1.0). Funnel long, broad-based; extends to anterior rim of eye; FuLI males 27.0–28.4–29.9 (SD, 2.1), females 29.5–31.2–32.3 (SD, 1.0). Funnel free portion approximately one-third funnel length: FFul males 11.2–12.7–14.1 (SD, 2.0), females 11.8–14.4–18.5 (SD, 2.7). Funnel organ dorsal elements inverted V-

Table 6. Distinguishing features of nominal *Sepiella* species. For non-Australian material, information was obtained from: Adam (1939), Adam and Rees (1966), Khromov *et al.* (1998), Nesis (1987), Okutani (1995) and Roelvelde (1972). 'Broad' refers to the dorso-ventral breadth of the cuttlebone. For abbreviations, see Table 1. Only those characters for which information was available for most species are included. * - species of uncertain status, M - males, F - females, m - metres. † - minimum depth not known.

Species	Patches at base of fins	CIRC	CbW/CbL	Broad cuttlebone	Maximum size (mm ML)	Depth range	Type locality	Distribution
<i>S. cyanea</i> Robson, 1924	+	10-14	29-33%M 30-36%F	+	80	? - 75m †	South Africa 29°17'S 31°33'E	South Africa - Port Elizabeth to 26°N of Mozambique and Madagascar
<i>S. inermis</i> Orbigny, 1848	+	12-24 13-20	33-43%	+	125	? - 40m †	Indian Ocean	Persian Gulf - southern part of Red Sea to mouth of Zambezi River, east to eastern Indonesia, Gulf of Tonkin
<i>S. japonica</i> Sasaki, 1929	-	16-32 >20 (usually)	30-35%	+	200	? - 50m †	Japan	Japan (central Honshu) to China (Canton), Philippines
<i>S. mangkangunga</i> sp. nov	-	12-15M 14-15F	27-31%M 23-33%F	+	58M 58F	1.1 - 3.3m	Australia	Northern Australia, 12°48'S 131°21'E - 13°14'S 130°57'E
<i>S. ocellata</i> Pfeffer, 1884*	+	8-10	20-25%	+	50	?	Java	Known only from type
<i>S. ornata</i> (Rang, 1837)	+	10-14	24-27%M 27-30%F	+	100	? - 150m † usually > 50m	Gulf of Guinea	West Africa - Cape Blanco to Cape Frio
<i>S. weberi</i> Adam, 1939	+	8M 7-10F	21-31%M 30-33%F	-	60M 69F	surface - 88m	Timor & Soemba	Indonesia - northern Australia, 8°35'S 126°00'E - 19°35'S 117°14'E

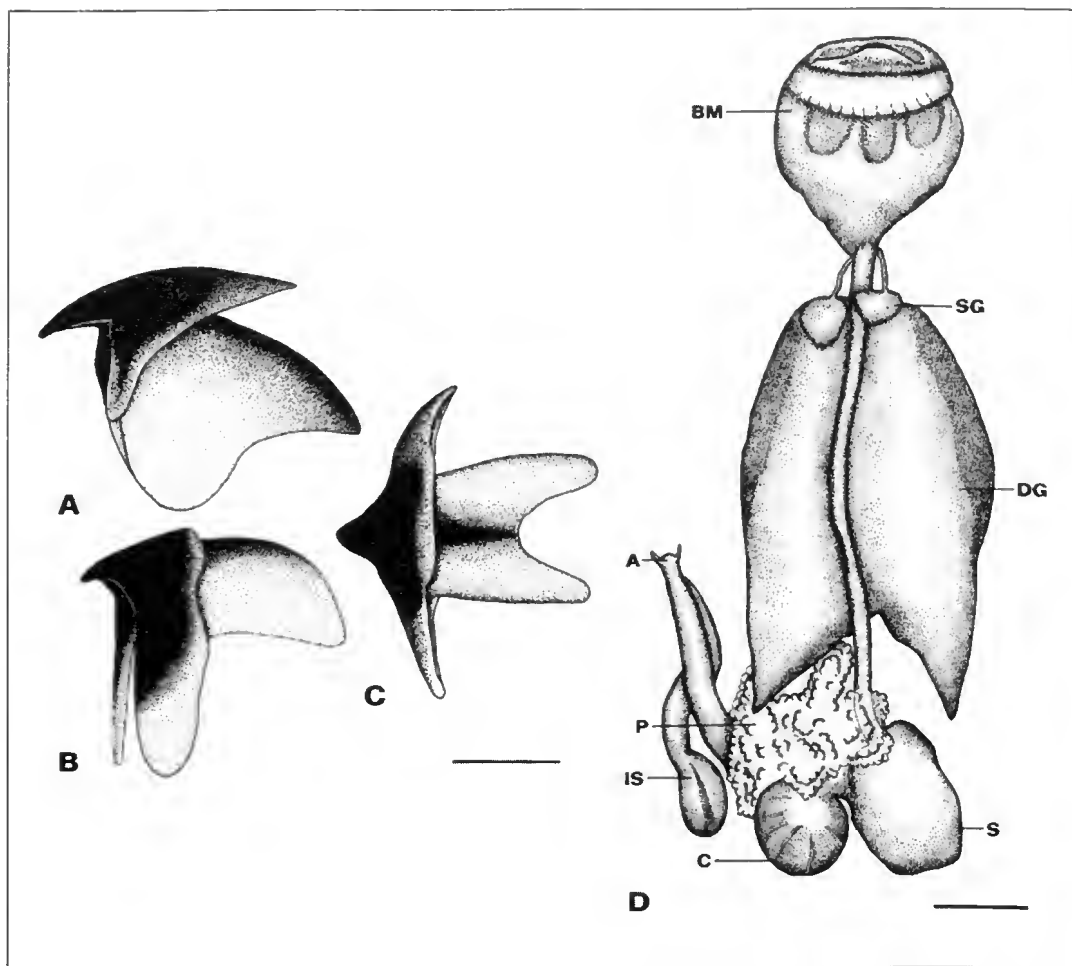


Fig. 6. *Sepiella mangkangunga* sp. nov.; A, upper beak, lateral view; B, lower beak, lateral view; C, lower beak, ventral view (A–C, female paratype, MV F80992, 54.7 mm ML, scale bar 2 mm); D, digestive tract, dorsal view, male, MV F65573, 37.7 mm ML, scale bar 3 mm (A – anus; BM – buccal mass; C – caecum; DG – digestive gland; IS – ink sac; P – pancreas; S – stomach; SG – salivary gland).

shape with low medial swelling and small papilla in front; ventral elements oval with acute anterior tip (Fig. 13A). Mantle-locking cartilage curved, with triangular tubercle; funnel-locking cartilage with depression corresponding to tubercle (Fig. 13B). Head short; HLI males 29.4–30.1–30.8 (SD, 1.0), females 27.1–29.6–31.6 (SD, 1.5); slender, narrower than mantle; HWI males 40.0–40.2–40.4 (SD, 0.3), females 32.5–36.9–41.0 (SD, 3.5). Eyes moderate size; EDI males 11.8–12.1–12.4 (SD, 0.4), females 12.6–13.4–14.6 (SD, 0.7); ventral eyelids present.

Male and female arms subequal in length (Table 8). Arm length index of longest arms in males (ALI4) 65.1–65.2–65.2 (SD, <0.01), females (ALI4) 37.9–42.8–46.9 (SD, 3.7). Protective membranes in both sexes wide, well developed; normal, not thickened. Distal arm tips in both sexes not markedly attenuate. Arm suckers tetraserial in both sexes. Two median series of suckers larger than dorsal and ventral marginal series in males; larger than female arm suckers (Table 8). Chitinous rims of arm suckers with marked sexual dimorphism. In males, distal margin of inner ring with 12–14 elongate,

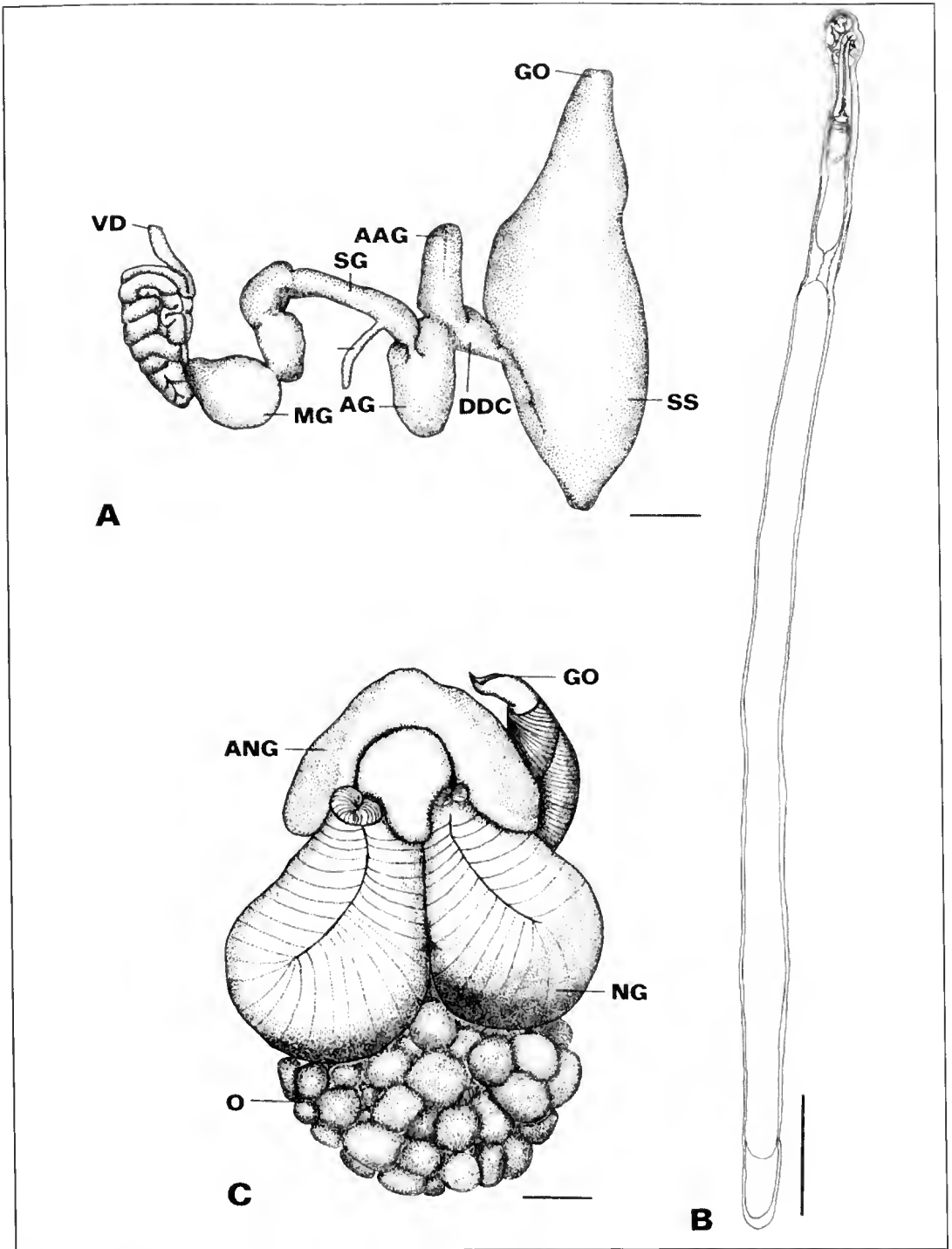


Fig. 7. *Sepiella mangkangunga* sp. nov.: **A**, male genital duct (testis not shown), paratype, MV F80992, 45.8 mm ML, scale bar 2 mm (AAG – appendix of accessory gland; AG – accessory gland; CC – ciliated canal; DDC – distal deferent canal; GO – genital orifice; MG – mucilaginous gland; SG – spermatophoric gland; SS – spermatophoric sac; VD – vas deferens); **B**, spermatophore, male, NTM P11116, 57.2 mm ML, scale bar 0.5 mm; **C**, female genital duct NTM P11116, 54.6 mm ML, scale bar 2 mm (ANG – accessory nidamental gland; GO – genital opening; NG – nidamental gland; O – ovary).

Table 7. Measurements (mm), counts and indices of 3 mature male and 7 mature female *Sepiella weberi* Adam. M – male, F – female.

Museum Reg. No.	NMV F65579 M	NMV F65571 M	ZMA Moll2.39.002 M	NMV F71713 F	NMV F71713 F	NMV F65575 F	NMV F71713 F	NMV F71713 F	NMV F65575 F	ZMA Moll3.39.001 F
ML	44.5	56.8	59.7	48.0	50.6	50.8	51.5	54.2	58.0	69.3
AMHI	11.5	12.3	10.0	10.2	8.9	8.7	12.0	12.9	10.9	10.4
VMLI	82.5	85.6	85.6	85.6	85.0	84.8	82.5	85.8	80.2	86.0
MWI	56.2	52.8	45.2	55.2	50.4	53.7	53.4	-	45.0	39.4
FWI	10.3	12.5	14.4	12.7	15.8	-	11.3	10.0	13.3	15.3
AFII	13.5	11.4	10.0	16.9	10.9	9.8	15.5	12.9	11.2	8.4
PFII	4.5	-	3.3	4.2	2.0	4.1	3.9	4.6	-	2.3
FuLI	27.0	29.9	26.0	32.3	30.6	31.5	31.1	29.7	31.9	20.9
FFuI	11.2	14.1	18.4	15.6	15.8	11.8	12.6	18.5	12.1	14.7
HLI	30.8	29.4	28.5	29.2	31.6	29.9	29.3	30.4	27.1	20.0
HWI	40.4	40.0	40.4	41.0	34.6	40.9	35.9	32.5	36.2	38.8
EDI	12.4	11.8	11.8	13.5	14.6	12.8	12.6	13.3	13.4	12.3
AL1I	40.4	38.7	33.5	35.4	33.6	40.4	38.8	35.1	29.3	34.6
AL2I	48.3	44.0	39.4	41.7	33.6	37.4	35.9	34.1	31.0	36.8
AL3I	53.9	54.6	44.4	43.8	37.5	35.4	40.8	36.9	34.5	36.1
AL4rI	65.2	65.1	54.4	46.9	39.5	41.3	46.6	44.3	37.9	38.2
AL4II	-	54.6	48.6	-	-	-	-	-	-	-
AS1In	1.84	1.85	1.59	1.56	1.28	1.48	1.46	1.42	1.47	1.44
AS2In	1.69	1.62	1.59	1.56	1.13	1.57	1.46	1.38	1.38	1.40
AS3In	2.13	1.85	1.54	1.77	1.38	1.48	1.46	1.42	1.21	1.10
AS4rIn	1.84	1.76	1.88	1.40	1.23	1.57	1.46	1.38	1.41	1.15
ASC1	71	84	-	98	72	104	98	110	94	-
ASC2	60	80	-	100	80	112	88	116	94	-
ASC3	94	102	78	100	92	114	106	118	112	-
ASC4	89	100	80	100	98	102	106	121	100	-
AS41In	2.36	1.76	1.76	-	-	-	-	-	-	-
AS41mIn	0.67	0.56	0.50	-	-	-	-	-	-	-
CIL	24.7	25.5	-	28.1	19.8	29.5	27.2	26.8	24.1	-
CIRC	8	8	-	8	9	7	8	8	8	10
TrRC	46	38	-	42	38	41	46	44	38	42
CISI	0.56	0.44	-	0.56	0.40	0.49	0.49	0.46	0.55	0.43
CISdI	0.49	0.35	-	0.52	0.30	0.53	0.39	0.41	0.43	0.36
CISvI	0.45	0.35	-	0.56	0.40	0.49	0.43	0.46	0.52	0.36
GiLC	-	27	28	27	28	27	27	-	-	29
GiLI	40.9	35.9	36.2	36.3	33.6	29.7	35.9	-	34.8	30.3
SpLI	10.1	7.9	10.0	-	-	-	-	-	-	-
SpWI	0.27	0.21	0.16	-	-	-	-	-	-	-
EgLI	-	-	-	4.2	4.5	5.5	4.8	4.6	4.8	-
CbL	43.9	56.9	56.1	50.0	51.0	51.1	52.0	55.8	55.0	-
CbWI	30.8	21.4	31.4	30.6	31.6	31.9	32.7	30.5	32.7	-
CbBI	11.4	9.7	-	11.4	11.4	12.5	11.1	10.7	11.1	-
StZI	45.6	61.5	50.3	45.0	60.8	60.7	50.0	48.4	61.8	-
LoLI	41.0	32.5	40.8	45.0	31.4	33.3	38.5	34.1	30.9	-
LoLStz(%)	90.0	52.9	81.2	100.0	51.6	54.8	76.9	70.4	50.0	-

pointed tooth-like processes (Fig. 12C, D), proximal margin smooth (Fig. 12C); in females, distal half of inner ring with two to three rows tooth-like structures (Fig. 14A, C), proximal margin of inner ring with blunt projections (Fig. 14B); infundibulum in both sexes with 11–15 rows of hexagonal processes, with pegs on innermost rows, outer processes without pegs (Figs 12C, 14A–B). In males, infundibular processes on inner margin of toothed side of ring narrow, elongate (Fig. 12D). Sucker counts range from 60–121; females with higher average counts than males (Table 8).

Hectocotylus present in males, left ventral arm modified; sucker size reduced proximally (Fig. 13C), 11–12 rows of reduced suckers; suckers in two dorsal series smaller than remaining suckers; two dorsal series widely spaced, suckers markedly reduced; two ventral series close together, suckers alternate; maximum and minimum sucker diameters: ASIn4 1.76–2.06–2.36 (SD, 0.42), ASIn4m 0.12–0.14–0.16 (SD, <0.01). Oral surface of modified region wide, fleshy, with transversely grooved ridges; without distinct median furrow. Hectocotylised arm not markedly attenuate distally.

Tentacular club similar length in males and females; CILI males 24.7–25.1–25.5 (SD, 0.6), females 19.8–25.9–29.5 (SD, 3.5).

Club crescent-shaped; sucker-bearing face convex. Club with 7–10 suckers in transverse rows. CIRC males 8, females 7–10; 38–46 suckers in longitudinal series, TrRC males 38–42–46 (SD, 6), females 38–41–46 (SD, 3). Suckers all similar size, small (Fig. 15); CISI males 0.44–0.50–0.56 (SD, 0.09), females 0.40–0.49–0.56 (SD, 0.06); dorsal and ventral marginal longitudinal series of suckers similar in size; CISId males 0.35–0.42–0.49 (SD, 0.10), females 0.30–0.43–0.53 (SD, 0.09); CISIv males 0.35–0.40–0.45 (SD, 0.07), females 0.40–0.48–0.56 (SD, 0.06). Sucker dentition: half inner ring circumference in both sexes with elongate, rectangular processes (Fig. 14D), remaining half with blunt projections; infundibulum with approximately 7–10 hexagonal processes with elongate pegs; at periphery, processes smaller, flattened, without pegs. Swimming keel of club length equal to length of carpus (Fig. 15). Dorsal and ventral protective membranes not fused at base of club (Fig. 15); joined to stalk; dorsal and ventral membranes same length, terminating at posterior end of carpus; dorsal membrane forms shallow cleft at junction with stalk.

Gills with 27–28 lamellae per demibranch; GiLC males 27, females 27–27–28 (SD, 0.5). Gill length: GiLI males 35.9–38.4–40.9 (SD, 3.5), females

Table 8. *Sepiella weberi* Adam; ranges of arm length indices (ALI), arm sucker diameter indices (ASIn) and arm sucker counts (ASC) of 10 mature males and 10 mature females. min. = minimum, max. = maximum, SD = standard deviation.

	Males				Females			
	min.	mean	max.	SD	min.	mean	max.	SD
ALI1	38.7	<u>39.6</u>	40.4	1.2	29.3	<u>35.4</u>	40.4	3.9
ALI2	44.0	<u>46.2</u>	48.3	3.0	31.0	<u>35.6</u>	41.7	3.7
ALI3	53.9	<u>54.3</u>	54.6	0.5	34.5	<u>38.1</u>	43.8	3.5
ALI4	65.1	<u>65.2</u>	65.2	0.01	37.9	<u>42.8</u>	46.9	3.7
ASIn1	1.84	<u>1.85</u>	1.85	<0.01	1.28	<u>1.44</u>	1.56	0.09
ASIn2	1.62	<u>1.65</u>	1.69	0.05	1.13	<u>1.41</u>	1.57	0.16
ASIn3	1.85	<u>1.99</u>	2.13	0.20	1.21	<u>1.45</u>	1.77	0.18
ASIn4	1.76	<u>1.80</u>	1.84	0.06	1.23	<u>1.41</u>	1.57	0.11
ASC1	71	<u>77</u>	84	9	72	<u>96</u>	110	13
ASC2	60	<u>70</u>	80	14	80	<u>98</u>	116	14
ASC3	94	<u>98</u>	102	6	92	<u>107</u>	118	10
ASC4	89	<u>94</u>	100	8	98	<u>104</u>	121	8

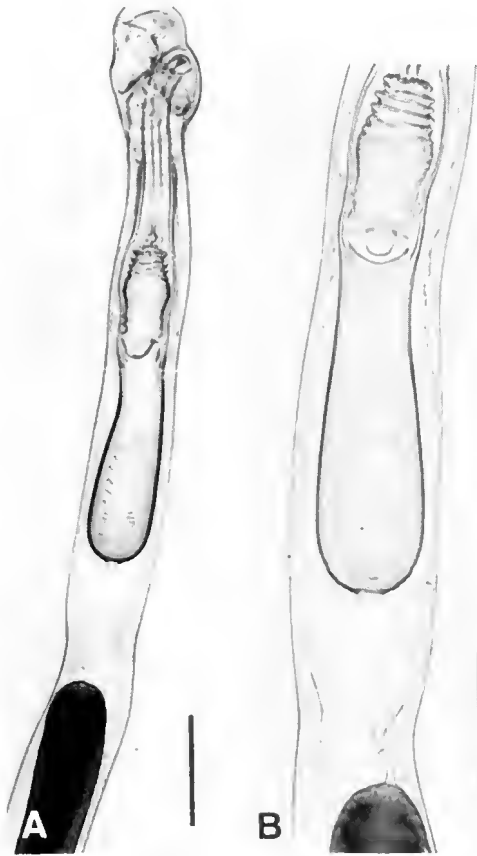


Fig. 8. *Sepiella mangkangunga* sp. nov.: **A**, spermatophore, oral end, male, NTM P16082, 57.2 mm ML, scale bar 0.3 mm; **B**, enlargement of ejaculatory apparatus, same specimen, scale bar 0.2 mm.

29.7–34.1–36.3 (SD, 2.6).

Buccal membrane without suckers. Upper beak (Fig. 16A) rostrum sharply pointed, long, curved, length greater than width, cutting edge straight; hood high above crest posteriorly; wings and hood narrow, short; jaw angle approximately 90° , slightly acute; hood dark brown, fading toward lateral ventral margin, crest dark brown medially, paler, brown laterally. Lower beak (Fig. 16B, C) rostral edge curved; rostrum protruding only slightly; hood low on crest; crest straight; no indentation on lateral wall edge; hood and wings width narrow; hood notch broad; wings widely spread; crest wide; rostrum pigmented dark brown, fading on wings, crest pigmented, darkest medially. Radula homodont; rhachidian teeth with

truncate bases; blunt, triangular, sides straight (Fig. 14E–F); first lateral teeth slightly longer than rhachidian teeth, with wide heels, asymmetrical with mesocone displaced toward centre of radula (Fig. 14E–F); second laterals longer than first, curved with broad heels; marginal teeth elongate, tapering, curved (Fig. 14E). Digestive tract: paired salivary glands approximately $\frac{1}{4}$ length of buccal mass; paired digestive glands large, located close together, with sub-triangular lobes posteriorly (Fig. 16D), ducts (not shown in Fig. 16) connecting digestive glands near midline with caecum, ducts with branched attached pancreatic tissue; oesophagus running dorsally along median junction of digestive glands, joining sac-like stomach immediately posterior to digestive glands; caecum disc-like, grooved in blunt V-shape anteriorly, surface lining finely pleated; intestine undifferentiated; ink sac and anal flaps well developed.

Male reproductive tract: testis on left posterior side of viscero-pericardial coelom; at distal end, convoluted vas deferens (Fig. 17A) opening into broad, cone-shaped mucilaginous gland, then narrower, curved, spermatophoric gland. Close to junction with lobe-shaped accessory gland and gland appendix, delicate ciliated canal joining spermatophoric gland; distal deferent canal connects appendix of accessory gland to spermatophoric sac; genital orifice opening dorsal to left gill in anterior end of mantle cavity. Spermatophores: (Figs 17B, 18A, B) cement body bipartite; aboral end cylindrical, tapering toward oral end, connecting to sperm reservoir via narrow duct extending from nipple-like tip of cement body, connecting to oral end by a distinct fold; oral end narrower than aboral end, tapering; ejaculatory apparatus coiled, extending into oral dilation of spermatophore. Spermatophores 4.5–6.0 mm long (SD, 0.7), 0.10–0.12 mm wide (SD, 0.01); SpL1 7.9–9.3–10.1 (SD, 1.2); SpWI 0.16–0.21–0.27 (SD, 0.05).

Female reproductive tract: ovary hanging from dorsal wall of posterior viscero-pericardial coelom. Oviduct thin-walled, continuous with body cavity; distally with thickened, glandular walls (oviducal glands). Nidamental glands in mature animals



Fig. 9. *Sepiella mangkangunga* sp. nov.: **A**, cuttlebone, dorsal view, female paratype, NTM P16082, 52.2 mm ML, scale bar 5 mm; **B**, cuttlebone, ventral view, same specimen; **C**, cuttlebone, lateral view same specimen, scale bar 5 mm; **D**, posterior end of cuttlebone, ventral view, same specimen, scale bar 2 mm (n.b. bone damaged on right side with evidence of repair).

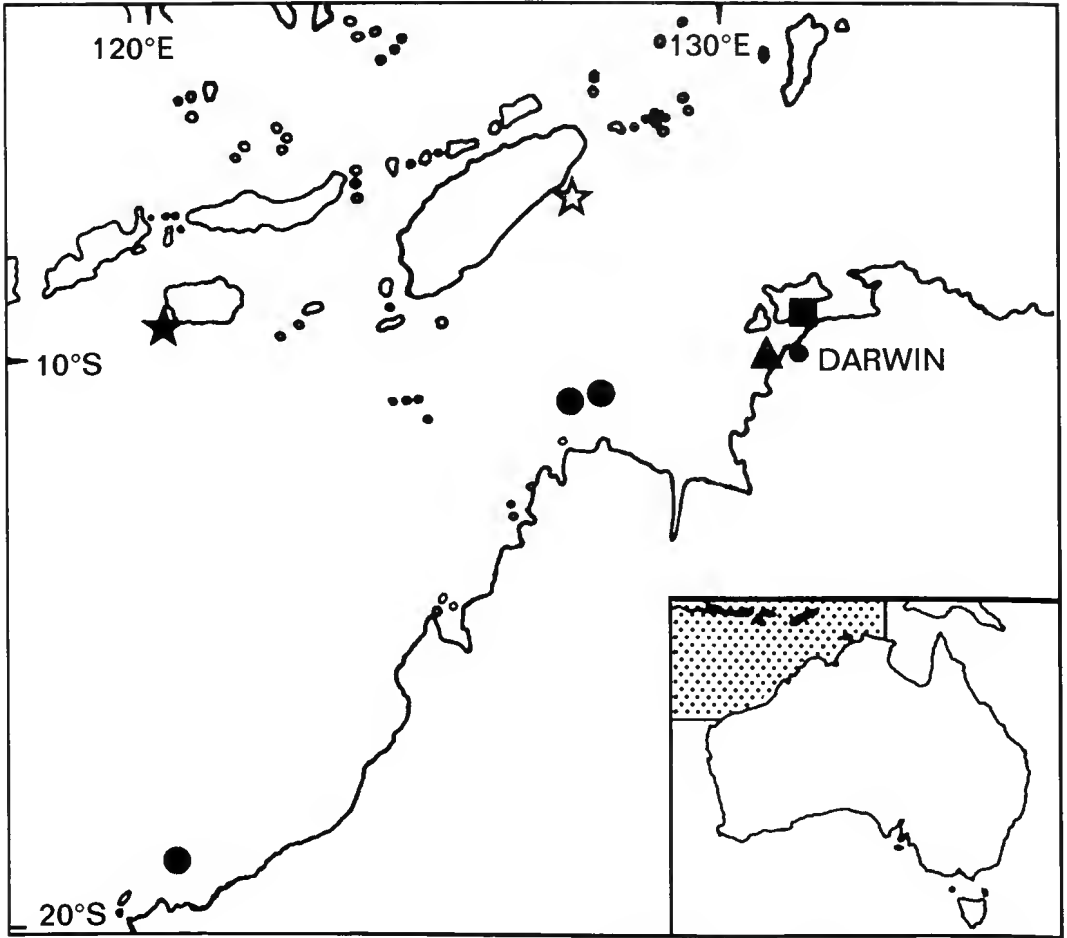


Fig. 10. Distributions of *Sepiella mangkangunga* sp. nov. (triangle), and *Sepiella weberi* Adam, 1939 (solid dots). The open star indicates the collection locality of the male, and the closed star the collection site for the female *Sepiella weberi* syntype. The solid square indicates the type locality of *Sepiella melwardi*.

occupying large portion of ventral side of mantle cavity. Accessory nidamental glands anterior to nidamental glands (Fig. 17C). Eggs spherical, 2.0–2.8 mm diameter (SD, 0.3); EgDI 4.2–4.7–5.5 (SD, 0.2).

Subdermal cartilaginous layer between cuttlebone and skin absent. Cuttlebone length approximately equal to mantle length; outline oblong (Fig. 19A, B); CbL males 43.9–50.4–56.9 (SD, 9.2), females 50.0–52.5–55.8 (SD, 2.4); CbWI males 21.4–26.1–30.8 (SD, 6.6), females 30.5–31.7–32.7 (SD, 1.0); not strongly convex in lateral view (Fig. 19C); CbBI males 9.7–10.3–11.0 (SD, 0.6), females

10.7–11.4–12.5 (SD, 0.6). Bone acuminate, acute anteriorly; bluntly rounded posteriorly; strongly recurved ventrally. Dorsal surface creamy white; convex medially, flat laterally; texture smooth, not pustulose. Dorsal median rib present, indistinct, broadening anteriorly; lateral ribs absent. Chitin surrounding entire margin of cuttlebone. Spine absent. Striated zone convex; StZI males 45.6–53.5–61.5 (SD, 11.3), females 45.0–54.4–61.8 (SD, 7.5). Last loculus convex (Fig. 19C); LoLI males 32.5–36.8–41.0 (SD, 6.0), females 30.9–35.5–45.0 (SD, 5.4); approximately 2/3 length of striated zone at midline,

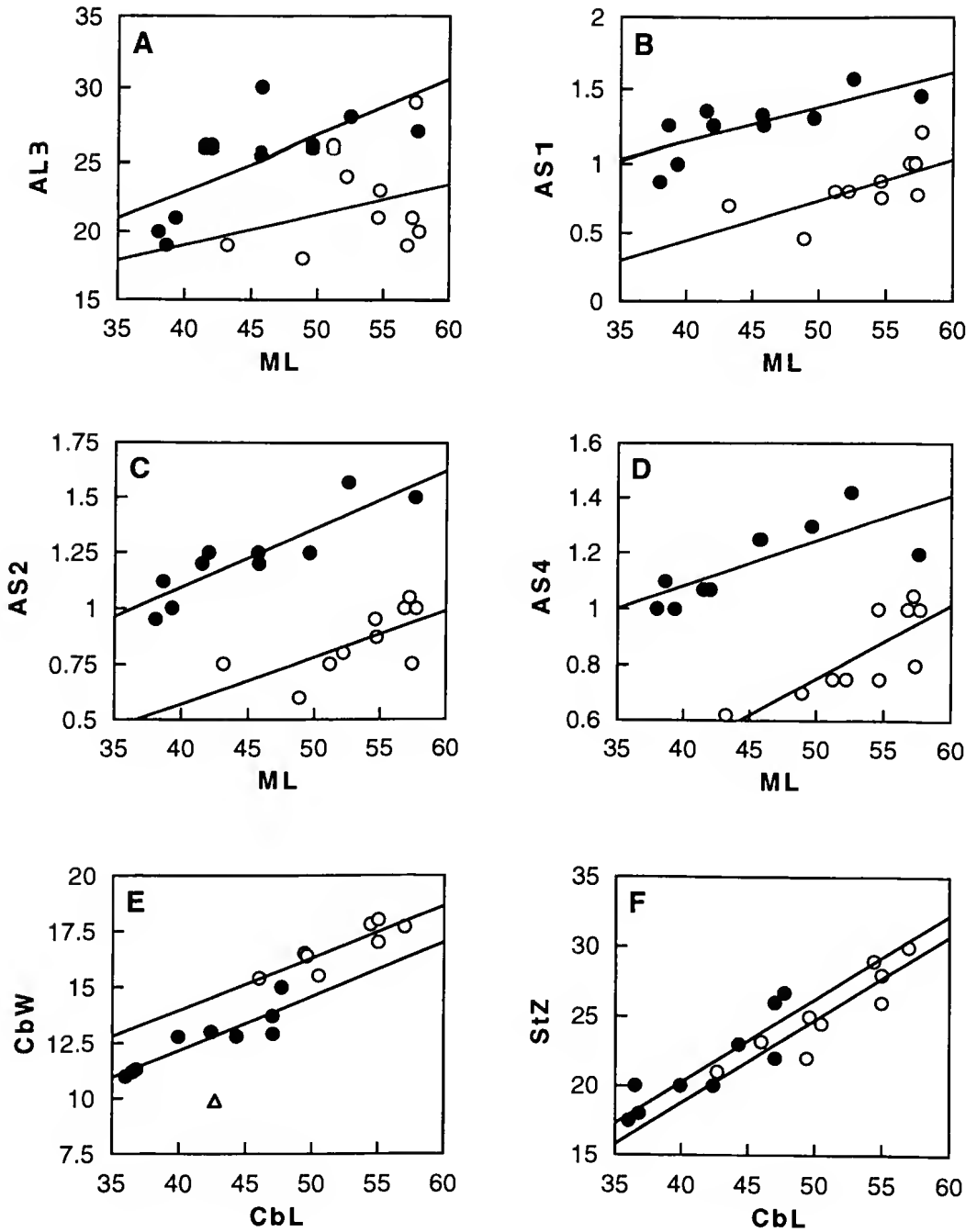


Fig. 11. Sexual dimorphism in *Sepiella mangkangunga* sp. nov. A, AL3 vs ML; B, AS1 vs ML; C, AS2 vs ML; D, AS4 vs ML; E, CbW vs ML; F, StZ vs ML. For regression formulae and comparison of lines refer to Table 5. Solid circles = males, open circles = females, open triangle (E) female – outlying value not included in the regression equation. For abbreviations see Table 1.

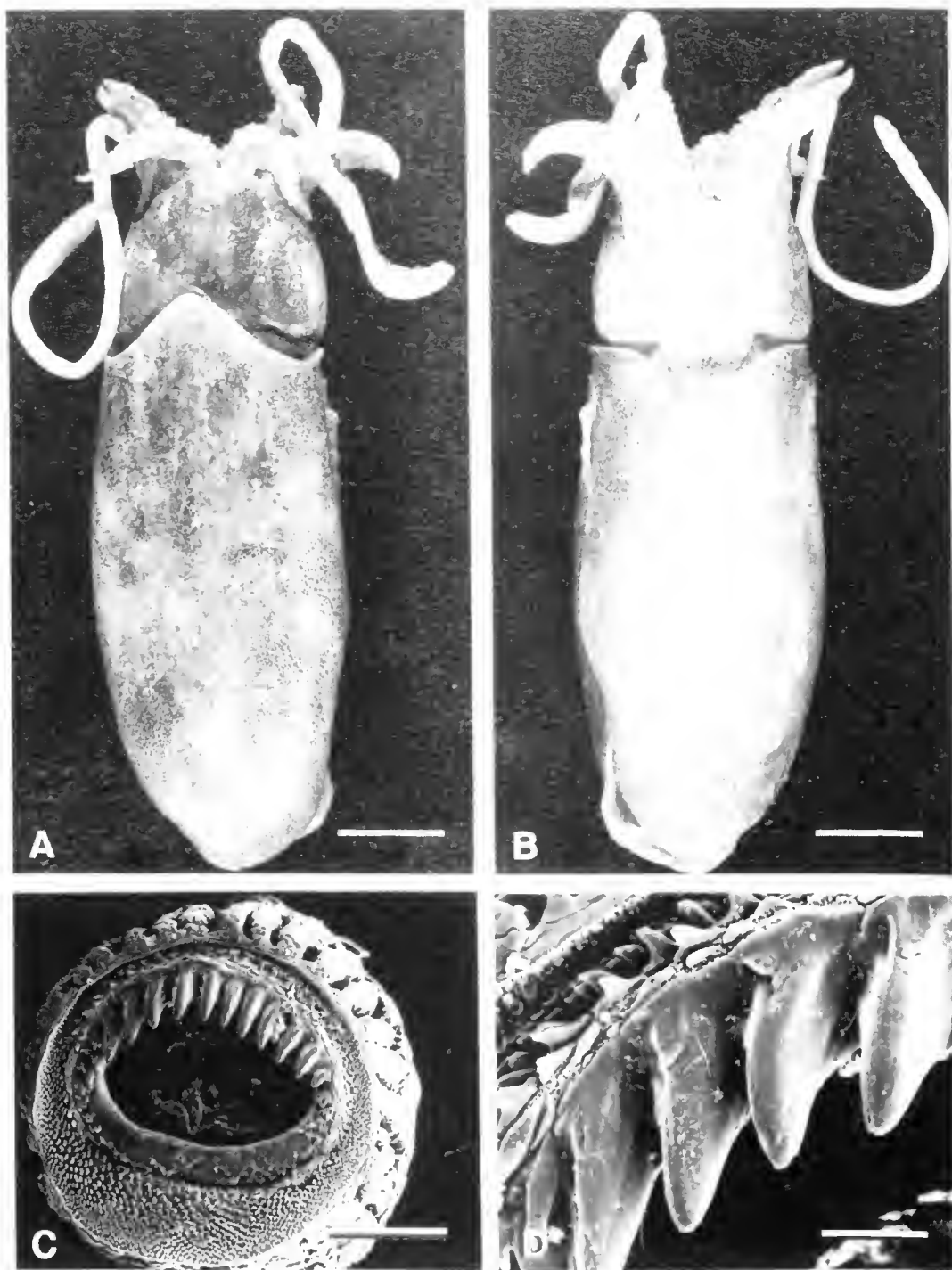


Fig. 12. *Sepiella weberi*: A, dorsal view, female, MV F65575, 54.3 mm ML, scale bar 10 mm; B, ventral view same specimen; C, arm 2 sucker, male, MV F65571, 56.8 mm ML, scale bar 200 μ m; D, enlargement of sucker rim, same specimen, scale bar 40 μ m.

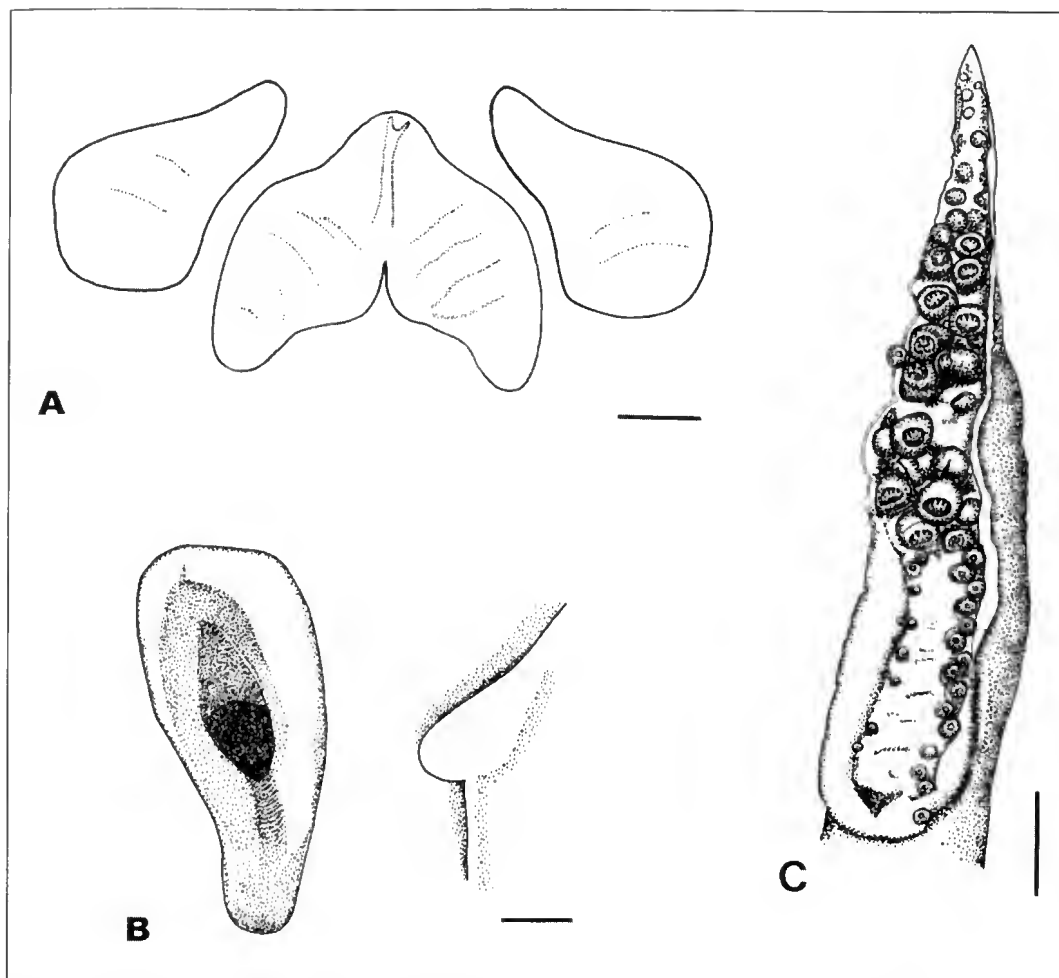


Fig. 13. *Sepiella weberi*: **A**, funnel organ, female, MV F65575, 47.1 mm ML, scale bar 2 mm; **B**, funnel locking cartilage (left), and mantle locking cartilage (right), male syntype, ZMA Moll.2.39.002, 59.7 mm ML, scale bar 1 mm; **C**, hectocotylus, male syntype, ZMA Moll.2.39.002, scale bar 2 mm.

LoL/StZ(%) males 52.9–71.4–90.0 (SD, 26.3), females 50.0–67.3–100.0 (SD, 19.3), loculus extending posteriorly as narrow margin on each side of striated zone. Sulcus extending entire length of cuttlebone; shallow, narrow; flanked by rounded ribs. Last loculus with shallow median indentation, not very pronounced. Anterior striae inverted U-shape, slightly wavy. Limbs of inner cone short, extending anteriorly to junction of striated zone and posterior termination of last loculus. Inner cone limbs uniform width, narrow; thickened slightly; not raised to form ledge posteriorly (Fig. 19D). Outer cone chitinous,

spatulate, expanded; narrow anteriorly, broadening posteriorly; postero-lateral wall without, or with very weak indentation in both sexes; limbs expanded, extending posteriorly beyond inner cone, recurved ventrally (Fig. 19C–D).

Papillae absent. Colour (alcohol preserved specimens): head and arms purplish brown; dorsal mantle pale, peppered with scattered purple-black chromatophores (Fig. 12A); paired dorsal eye spots absent. Fins pigmented; with five to six oval orange-pink spots at base of fins in both sexes, spots slightly larger, and more prominent in males. Ventral pigment present, pale (Fig. 12B).

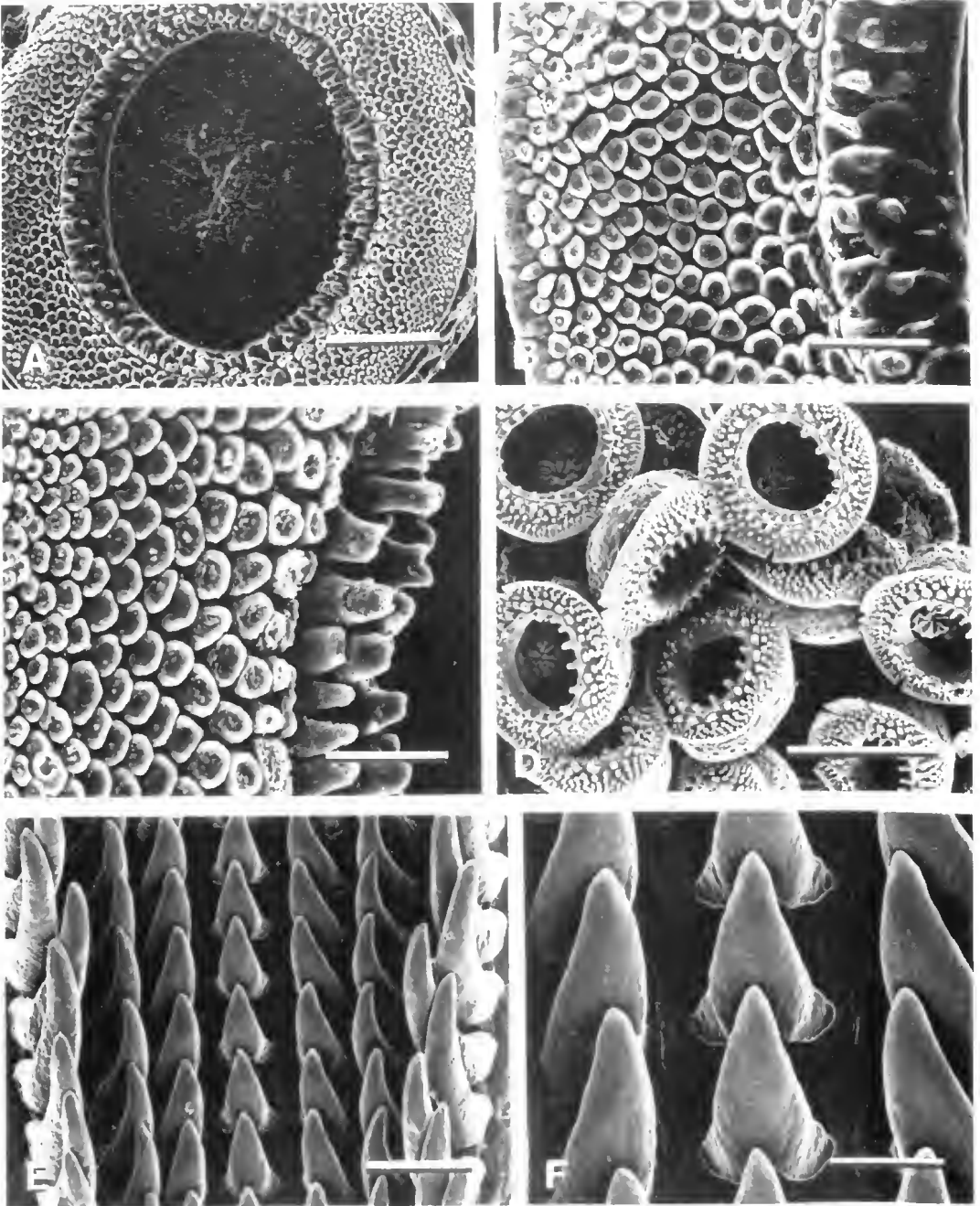


Fig. 14. *Sepiella weberi*: A, sucker rim, arm 2, female, MV F71713, 49.7 mm ML, scale bar 100 µm; B, enlargement of arm sucker rim, same specimen, scale bar 10 µm; C, enlargement of inner side of arm sucker rim, same specimen, scale bar 10 µm; D, club suckers, female, MV F65575, 54.3 mm ML, scale bar 200 µm; E, radula, female, MV F71713, 49.7 mm ML, scale bar 200 µm; F, enlargement of first lateral (left) and rhachidian teeth, same specimen, scale bar 100 µm.

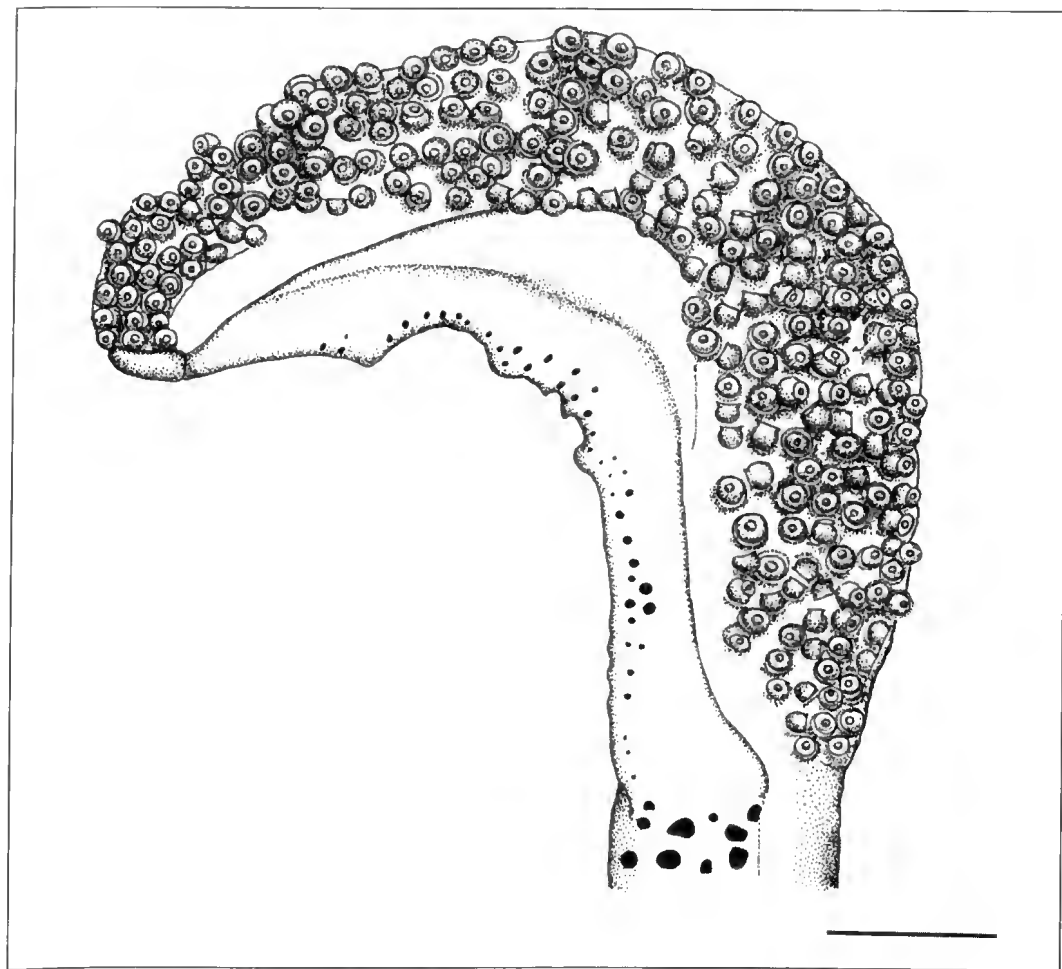


Fig. 15. *Sepiella weberi*: tentacular club, female, MV F65575, 50.0 mm ML, scale bar 2 mm.

Distribution. Indonesia (Timor – Soemba) 8°35'S 126°00'E – 10°S 119°56'E to northwestern Australia 12°39'S 127°03'E – 19°35'S 117°14'E (Fig. 10). Depth range surface to 88 m (see Remarks).

Remarks. The female syntype from Soemba, Indonesia (ZMA Moll.3.39.001) differs slightly from all remaining specimens in having the swimming keel slightly shorter, rather than equal to the carpus in length. It does not differ in other respects to the other material examined. Differences between *Sepiella weberi* and *S. mangkangunga* sp. nov. are given in the Remarks section of *S. mangkangunga* sp. nov. above. Table 6 shows some characters which differ between all nominal *Sepiella* species. In contrast to *S.*

weberi, in all other *Sepiella* species, the ventral side of the cuttlebone is strongly convex medially. In other characters, *S. weberi* is very similar to *S. cyanea*, differing primarily in the shape of the cuttlebone. The posterior end of the striated zone is more acuminate in *S. cyanea* than in *S. weberi* (Adam and Rees 1966). The shape of the bone differs also from *S. ocellata*. The bone of the latter species is narrower, and uniform in width throughout its length, while in *S. weberi* the bone is wider in the posterior half. The bone in *S. inermis* is much wider than that of *S. weberi*, and distinctly oval in outline, rather than oblong. The sulcus is deeper and much more well defined in *S. inermis* than in *S. weberi*, and *S. inermis* has

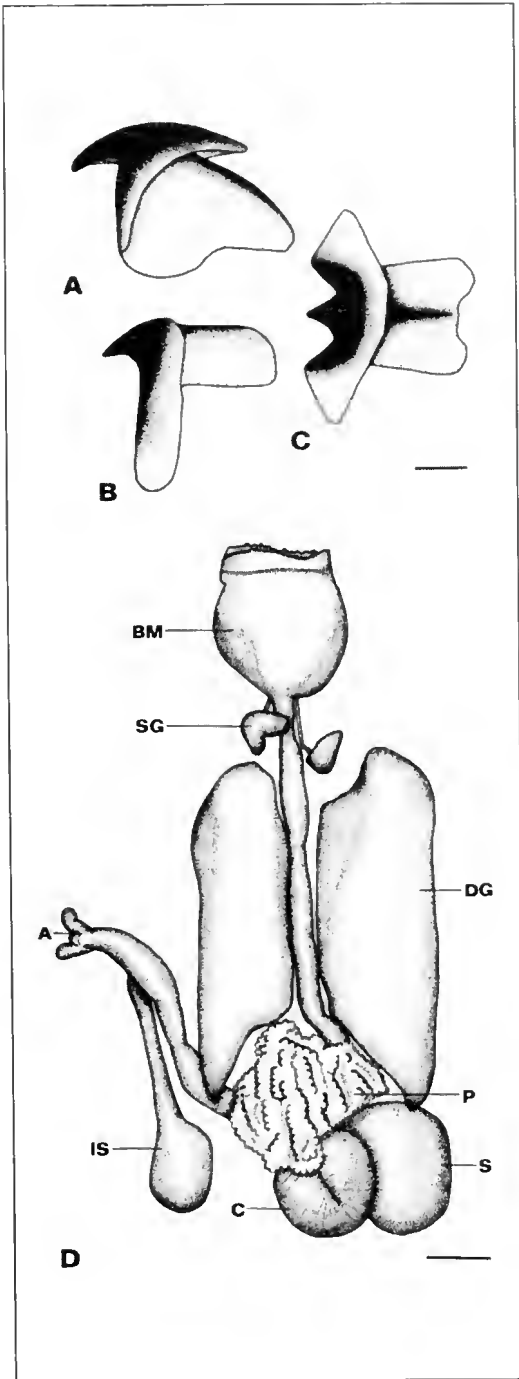


Fig. 16. *Sepiella weberi*: A, upper beak, lateral view; B, lower beak, lateral view; C, lower beak, ventral view (A-C, male, MV F65579, 44.5 mm ML, scale bar 2 mm); D, digestive tract, dorsal view, female, MV F65575, 53.2 mm ML, scale bar 2 mm, abbreviations as in Figure 6D.

12–20, while *S. weberi* has 7–10 club suckers in transverse rows.

The Australian *S. weberi* were all collected between 88 and 77 m depth, while the syntypes from Indonesia were found in shallower water. The female syntype was collected at 18 m. The male syntype was caught at the surface at night following attraction to lamp light, suggesting there may be a nocturnal migration into shallower waters.

Key to the species of *Sepiella* found in Australian waters

Dorsal mantle with ovoid spots at base of each fin. Tentacular club with 12–15 suckers in transverse rows; swimming keel shorter than carpus. Cuttlebone strongly convex in lateral view *S. mangkangunga* sp. nov.

Dorsal mantle without ovoid spots at base of each fin. Tentacular club with 7–10 suckers in transverse rows; swimming keel terminates at level of carpus. Cuttlebone not strongly convex in lateral view *S. weberi* Adam

ACKNOWLEDGMENTS

We wish to thank I. Loeh (AM) and R. Moolenbeek (ZMA) for the loan of material. For help with scanning electron microscopy we are grateful for the help of F. Brink and D. Vowles at the E.M. Unit, Research School of Biological Sciences, Australian National University (ANU). Thanks also to J. Wilson (ANU) for assistance with photography. We thank Professor Adrian Gibbs for providing work space and facilities at the Research School of Biological Sciences in Canberra (ANU) to Amanda Reid, and we are grateful to the referees for their helpful comments on this manuscript. This work was made possible by a support grant from the Australian Biological Resources Study Program to C.C. Lu.

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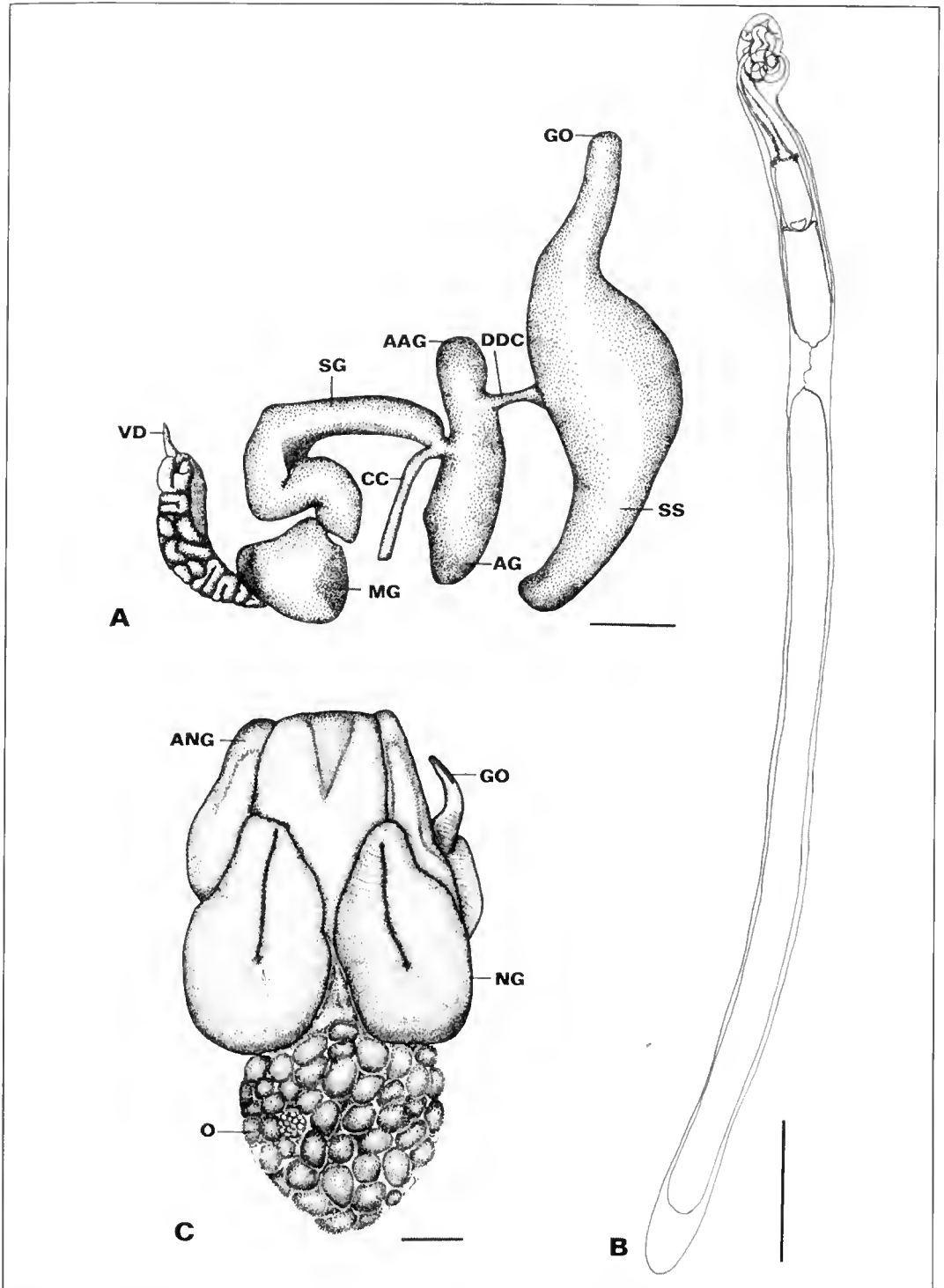


Fig. 17. *Sepiella weberi*: A, male genital duct MV F65579, 44.5 mm ML, scale bar 1 mm, abbreviations as in figure 7A; B, spermatophore, male, MV F65571, 56.8 mm ML, scale bar 0.5 mm; C, female genital duct MV F65575, 53.2 mm ML, scale bar 3 mm, abbreviations as in Figure 7C.

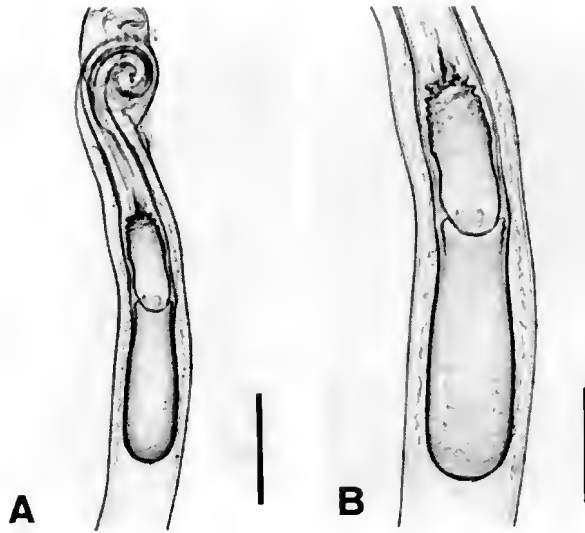


Fig. 18. *Sepiella weberi*: **A**, spermatophore, oral end, male, MV F65571, 56.8 mm ML, scale bar 0.3 mm; **B**, enlargement of ejaculatory apparatus, same specimen, scale bar 0.1 mm.

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Fig. 19. *Sepiella weberi*: A, cuttlebone dorsal view, female, MV F65575, 47.1 mm ML, scale bar 5 mm; B, cuttlebone ventral view, same specimen; C, cuttlebone lateral view, male, MV F65571, 56.8 mm ML, scale bar 5 mm; D, posterior end of cuttlebone, ventral view, female, MV F65575, 47.1 mm ML, scale bar 2 mm.

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Accepted 20 March, 1998

NEW RECORDS OF THE WATER MITE FAMILIES ANISITSIELLIDAE, MOMONIIDAE AND MIDEOPSIDAE FROM AUSTRALIA, WITH THE DESCRIPTION OF TWO NEW SPECIES (ACARI: ACTINEDIDA)

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ABSTRACT

Two new species of the water mite genus *Gretacarus*, *G. bifalcisetus* sp. nov. and *G. tuberipalpis* sp. nov., are described from the Northern Territory and Western Australia. *Momoniella australica* Cook is recorded for the first time from the Northern Territory and Western Australia. Finally, a new record is given for *Sigthoria nilotica* (Nordenskiöld) from the Northern Territory.

KEYWORDS: Acari, Actinedida, water mites, new species, Northern Territory, Western Australia, Australia

INTRODUCTION

Although the first water mite species from Australia was already described at the end of the 19th century, publications on water mites were scarce until the 1940s. The publication by Cook (1986), who described more than 200 new species, was a major leap forward in our knowledge of Australian water mites. Until recently, most publications dealt with the water mite fauna of eastern and southeastern Australia, and very few species were known from northern and western Australia. This paper is part of a series which aims to describe the water mite fauna of northern and western Australia. For each family new records will be given and, if appropriate, new species will be described.

In this paper the water mite families Anisitsiellidae, Momoniidae and Mideopsidae are treated, all small families in Australia. The Anisitsiellidae are represented in Australia by four genera, viz. *Sigthoria* Koenike, *Auisitsiellides* Lundblad, *Rutacarus* Lundblad and *Manersella* K. Viets, with one, five, two and one species respectively (Harvey 1990c). The Momoniidae are represented in Australia by two genera, viz. *Partidomomonina* Cook and *Momoniella* Viets, both with two species (Cook 1986; Harvey 1990a). The family Mideopsidae is represented by four genera,

viz. *Gretacarus* K.O. Viets, *Penemideopsis* Cook, *Guineaxonopsis* Imamura and *Tillia* Harvey, with eleven, three, one and one species respectively (Cook 1986; Harvey 1990b, 1996). So far, only the genera *Sigthoria*, *Penemideopsis* and *Tillia* have been reported from the Northern Territory and Western Australia.

In this study new records are presented from the Northern Territory and Western Australia, and two new species are described from the genus *Gretacarus*.

MATERIALS AND METHODS

All material has been collected by the author. Northern Territory holotypes and paratypes have been deposited in the Northern Territory Museum (Darwin) (NTM), Western Australia holotypes and paratypes in the Western Australian Museum (Perth) (WAM). Further, paratypes and all non-type material have been deposited in the Zoological Museum of the University of Amsterdam (ZMA).

Measurements of palp and leg segments are dorsal lengths. Measurements of paratypes are given in brackets. The following abbreviations have been used: PI-PV palp segments 1-5; I-leg-5 fifth segment of first leg. All measurements are in µm.

SYSTEMATICS

Sigthoria Koenike, 1907

Sigthoria Koenike, 1907: 127.

Sigthoria nilotica (Nordenskiöld, 1905)

Amasis niloticus Nordenskiöld. 1905: 9.

Material examined. ZMA, 8 ♂♂, 2 ♀♀, Douglas Hot Springs, Northern Territory, Australia, 31 July 1994.

Sigthoria nilotica is a widespread species, known from Asia and Africa, with one record from The Netherlands (Smit and Van der Hammen 1992). From Australia the species is known from the Northern Territory, Queensland and Victoria (Viets 1981; Harvey 1990c). The status of specimens from Queensland and Victoria has to be confirmed (Harvey 1990c). Maximum length of the males in this study is 572, and is larger than the data given by Harvey (1990c).

The locality of the new record is a very hot spring (main spring up to 60°C); the species is able to withstand high temperatures.

Momoniella Viets, 1929

Momoniella Viets, 1929: 236.

Momoniella australica Cook, 1986

Momoniella australica Cook, 1986: 284.

Momoniella australica – Smit 1992: 105.

Material examined. *Northern Territory.* ZMA, 1 ♂, 3 ♀♀, Radon Springs, Kakadu National Park, 19 July 1994; 1 ♀, pool at Twin Falls, Kakadu National Park; 2 ♂♂, plunge pool at Edith Falls, Katherine Gorge National Park.

Western Australia. ZMA, 1 ♀, pond at Dales Gorge, Hamersley Range National Park; 1 ♂, 8 ♀♀, Deep Reach Pool, Millstream-Chichester National Park, 15 August 1994; 4 ♀♀, western part of Deep Reach Pool, Millstream-Chichester National Park, 16

August 1994; 1 ♀, Crossing Pool, Millstream-Chichester National Park, 16 August 1994.

Remarks. Hitherto, the species has only been reported from eastern Australia (Tasmania, New South Wales, Queensland). Therefore, the records from the Northern Territory and Western Australia mean a considerable range extension of the species.

Gretacarus K.O. Viets, 1978

Gretacarus K.O. Viets, 1978: 90.

This is the first record of this genus from the Northern Territory and Western Australia. Females are difficult to recognize, and assignment of the females is based on association with the males. Females are therefore not always illustrated.

Gretacarus bifalcisetus sp. nov.
(Fig. 1A–F)

Type material. HOLOTYPE – WAM 97/3250 ♂, small streams originating in Chinderwariner Pool, Millstream-Chichester National Park, Western Australia, Australia, 15 August 1994 (WAM). PARATYPES – WAM 97/3251–5, 3 ♂♂, 2 ♀♀, and ZMA, 4 ♂♂, 2 ♀♀, same data as holotype.

Diagnosis. IV-leg-4 with two long, hyaline falcate setae, and one falcate setae which is contracted distally; dorsal margin of PIV with a small bump.

Description. *Male.* Dorsal and ventral shields present. Body 553 (534–563) long and 495 (500) wide. Dorsal shield 479 (446–485) long and 422 (422–430) wide. Second pair of glandularia on dorsum much closer together than other two pairs (Fig. 1E). Long ridges extending posteriorly of fourth coxal fields. Genital field 72 long, posterior part 48 wide. Genital field with approximately 30–31 acetabula, posterior part three rows wide, anterior part two rows wide (Fig. 1A). Lengths of PI–V: 43, 43, 31, 46, 22. Heavy seta of PIV saddle-shaped, on long tubercle; dorsal margin of PIV with small bump in the middle. PIII with a short, blunt seta on dorsal margin (Fig. 1B). Lengths of I-leg-4–6: 60, 70, 84 (measured

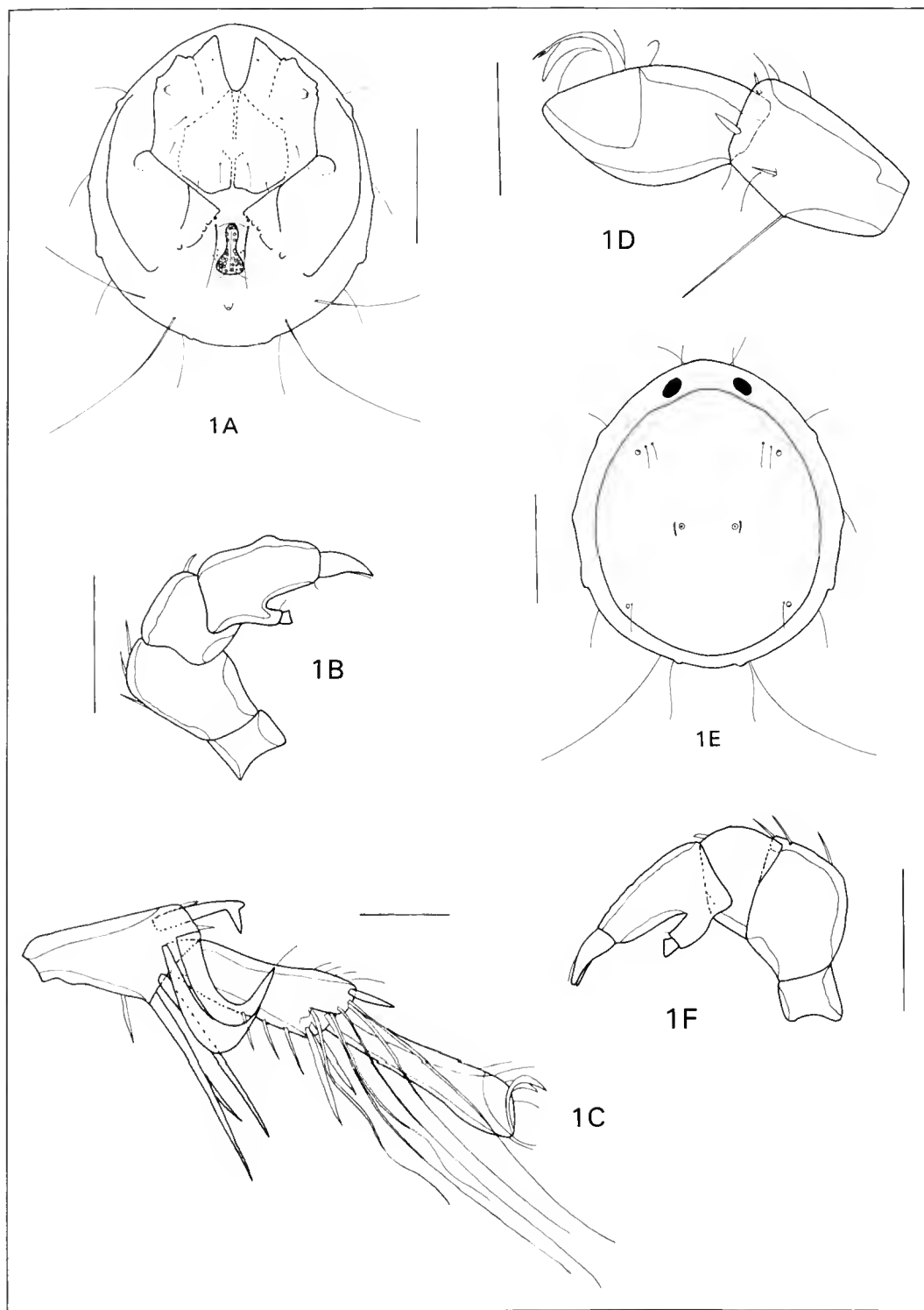


Fig. 1. *Gretacarus bifalcisetus* sp. nov., holotype ♂ **A**, ventral view; **B**, palp; **C**, IV-leg-5-6; **D**, I-leg-5-6; **E**, dorsal view; **F**, paratype ♀, palp. Scale lines: A and E, 200 µm; B–D and F, 50 µm.

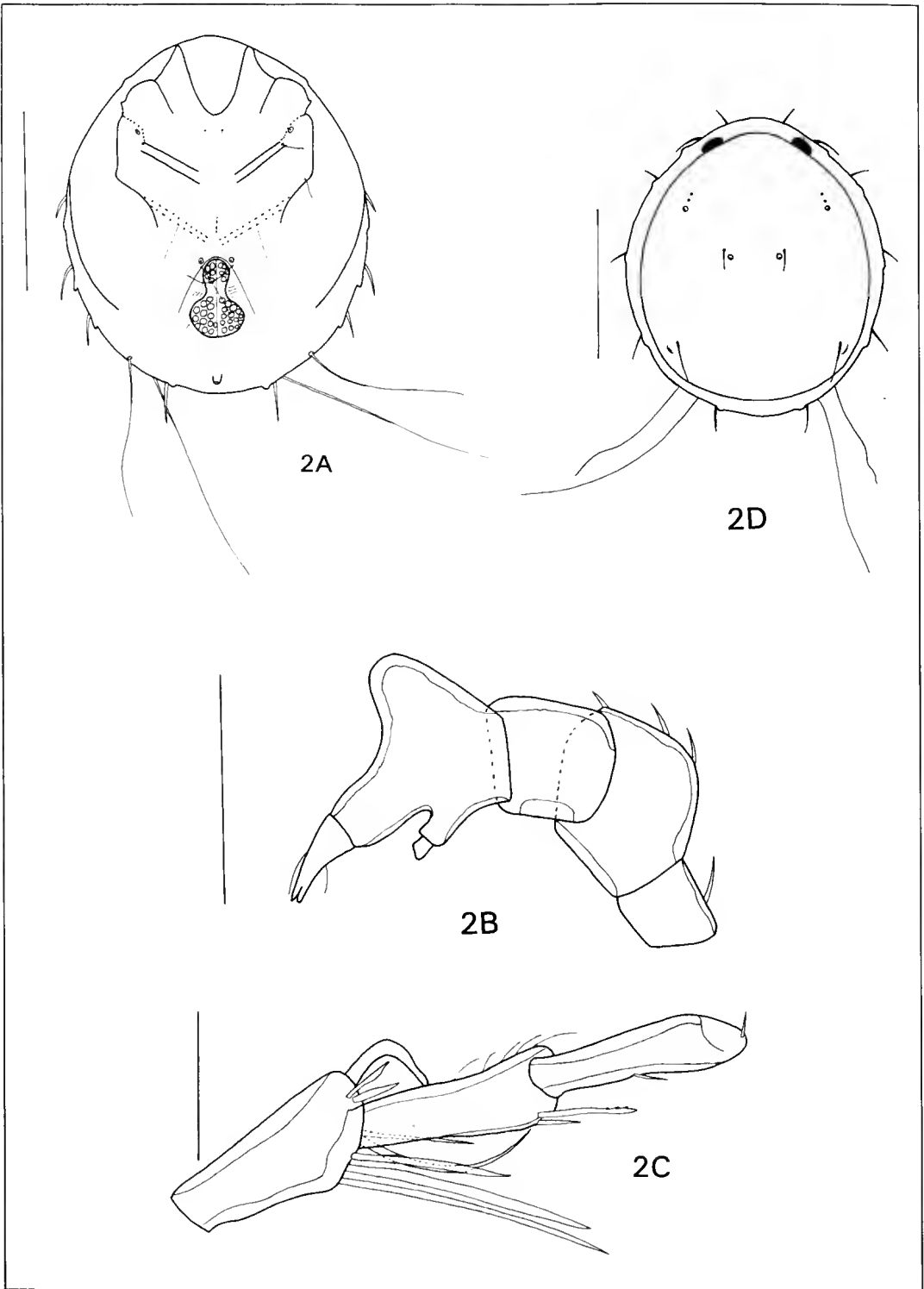


Fig. 2. *Gretacarus tuberipalpis* sp. nov., holotype ♂. A, ventral view; B, palp; C, IV-leg-4-6; D, dorsal view. Scale lines: A and D, 200 μ m; B and C, 50 μ m.

from anterior tip of segment). Lengths of IV-leg-4-6 86, 98, 115. IV-leg-4 with two long, hyaline falcate setae, and one falcate setae which is contracted distally (Fig. 1C). Claws of first and second legs with large clawlets (Fig. 1D); dorsal clawlet of these legs bifurcate. Third and fourth legs with swimming setae.

Female. Dorsal and ventral shields present. Body 553 (543) long and 514 (504–524) wide; dorsal shield 495 long and 446 wide. Coxoglandularia 2 anterior to genital field. Genital field 156 wide, gonopore 108 long. Genital plates two to three acetabula in width. Lengths of PIV: 19, 43, 31, 49, 22. Palp as in male, except PIV, which lacks small bump in dorsal margin, and ventral margin of the tubercle more bowed (Fig. 1F). Lengths of I-leg-5-6: 67, 91. Lengths of IV-leg-4-6: 89, 100, 110.

Remarks. Its closest relative is *Gretacarus expansisetus* Cook, which has a more or less similar genital field. The latter species has more acetabula (posterior part five rows wide), lacks the bump on PIV and has four widened seta on IV-leg-4. The female can probably not be separated from other females.

Etymology. Named for the two falcate hyaline setae of IV-leg-4.

***Gretacarus tuberipalpis* sp. nov.**

(Fig. 2A–D)

Type material. HOLOTYPE – ♂, Lily Ponds Falls, Katherine Gorge National Park, Northern Territory, Australia, 27 July 1994 (NTM). PARATYPES – NTM, 1♀ and ZMA, 1♂, 2♀♀, same data as holotype; WAM 97/3256, 1♂, pond at Kalamina Gorge near falls, Hamersley Range National Park, Western Australia, Australia, 13 August 1994.

Diagnosis. PIV of male dorsally with very large hump, IV-leg-4 of male with one falcate seta.

Description. *Male.* Dorsal and ventral shields present. Body 369 (398–553) long and 320 (369–514) wide; dorsal shield 339 long and 291 wide. Setae associated with lateroglandularia stout. Second pair of

glandularia on dorsum much closer together than other two pairs (Fig. 2D). Coxoglandularia 2 at same level of anterior margin of genital field. Ridges extending posteriorly from fourth coxal plates indistinct in holotype, but distinct in paratype from Western Australia. Gonopore 76 long, posterior part of genital field 53 wide. Genital field with 13–16 acetabula posteriorly and five acetabula anteriorly (Fig. 2A). Dorsal lengths of PI–PV: 17, 36, 29, 43, 21. PIV dorsally with unusual, very large hump; heavy seta on relatively short tubercle (Fig. 2B). Dorsal lengths of I-leg-4-6: 50, 48, 41; dorsal lengths of IV-leg-4-6: 74, 72, 58. IV-leg-4 dorsally with curved seta, enlarged anteriorly, and ventrally with thin hyaline curved seta (Fig. 2C, claw of holotype lost). Claws of first and second legs with large clawlets, dorsal clawlet of these legs bifurcate. Third and fourth legs with swimming setae.

Female. Dorsal and ventral shields present. Body 436 (398–417) long and 388 (359–378) wide; dorsal shield 378 long and 335 wide. Coxoglandularia 2 anterior to genital field. Genital field 170 wide, gonopore 125 long. Genital plates two acetabula in width. Lengths of PIV: 17, 36, 26, 42, 19. Palp without distinct characters, lacking large hump of PIV, while tubercle of ventral margin of PIV is longer. Lengths of I-leg-4-6: 48, 53, 48. Lengths of IV-leg-4-6: 80, 86, 89.

Remarks. No other species of the genus has PIV with such a large hump. Although there are some differences between the males from the Northern Territory and the male from Western Australia (size, ridges on fourth coxal plates), both have the same characteristic palp, and also the fourth leg and genital field are similar. They are therefore assigned to the same species. The female probably cannot be separated from other females.

Etymology. Named for the large hump of PIV.

ACKNOWLEDGMENTS

I am indebted to the Western Australian Department of Conservation and Land

Management (Como), the Australian National Parks and Wildlife Service (Darwin) and the Conservation Commission of the Northern Territory (Palmerston) for their permission to collect water mites in the national parks of Western Australia and the Northern Territory and to G.M. van der Pal for her assistance with the fieldwork.

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Accepted 14 April, 1998

NEW RECORDS OF THE WATER MITE FAMILY HYDRYPHANTIDAE FROM AUSTRALIA, WITH THE DESCRIPTION OF THREE NEW SPECIES (ACARI: ACTINEDIDA)

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ABSTRACT

Two new species of the water mite genus *Pseudohydrphantus*, *P. gracilipalpis* sp. nov. and *P. elongatus* sp. nov., and one new species of the genus *Cyclohydrphantus*, *C. occidentalis* sp. nov., are described from Northern Territory and Western Australia. New records are presented from already known species of the genera *Hydrphantus*, *Pseudohydrphantus* and *Diplodontus* from Northern Territory and Western Australia.

KEYWORDS: Water mites, new species, Northern Territory, Western Australia, Australia

INTRODUCTION

The water mite family Hydrphantidae is represented in Australia by nine genera (the number of species in brackets): *Hydrphantus* Koch (2), *Notopanisus* Besch (1), *Austrotrombella* Southcott (1), *Wandesia* Schechtel (2), *Tartarothys* Viets (1), *Pseudohydrphantus* Viets (11), *Cyclohydrphantus* Lundblad (2), *Diplodontus* Dugès (2) and *Mamersa* Koenike (1) (Lundblad 1947; Cook 1986; Harvey 1987, 1988a, 1988b, 1996). From Northern Territory only four species are known of the genera *Mamersa* and *Pseudohydrphantus*, and one species of the genus *Hydrphantus* has been reported from Western Australia.

In this study two new *Pseudohydrphantus* species are described from Northern Territory, and one new *Cyclohydrphantus* species from Western Australia. New records are presented of already known species from Northern Territory and Western Australia.

MATERIAL AND METHODS

All material has been collected by the author. Western Australian and Northern Territory holotypes and paratypes have been deposited in the Western Australian Museum (Perth) (WAM), and in the Museum and Art Gallery of the Northern Territory (Darwin) (NTM) respectively. Paratypes and all non-type material have been deposited in the

Zoological Museum of the University of Amsterdam (ZMA). Measurements are in µm, measurements of palp and leg segments are of dorsal margins. Measurements of paratypes are given in brackets. The following abbreviations have been used: PI-PV, palp segments 1-5; I-leg-5, fifth segment of first leg. For terminology of glandularia see Harvey (1988b).

SYSTEMATICS

Hydrphantus Koch, 1841

Hydrphantus Koch, 1841: 18.

Two species and one subspecies of this genus are known from Australia, both from the subgenus *Polyhydrphantus*. The genus has been recorded from Victoria, New South Wales, Queensland and Western Australia (Lundblad 1947; Cook 1986)

Hydrphantus (Polyhydrphantus) haliki Cook, 1986

Hydrphantus (Polyhydrphantus) haliki
Cook, 1986: 13.

Hydrphantus (Polyhydrphantus) haliki -
Smit 1992: 92.

Material examined. WESTERN AUSTRALIA. ZMA, 3 ♀♀, pond at Dales Gorge, Hamersley Range National Park, 12 August 1994.

Remarks. The species has been reported from New South Wales and Queensland, so the record from Western Australia means a considerable range extension of the species.

Pseudohydryphantes Viets, 1907

Pseudohydryphantes Viets, 1907: 130.

Fourteen species of *Pseudohydryphantes* have been described so far, of which eleven are known from Australia and New Zealand. With the two new species described in this paper, more than 80 % of the known species are from Australia and New Zealand.

***Pseudohydryphantes wangai*
Harvey, 1988**

Pseudohydryphantes wangai Harvey, 1988b: 21.

Material examined. NORTHERN TERRITORY. ZMA, 4 ♂♂, 25 ♀♀, pond at Jim Jim Creek, near Jim Jim campground, Kakadu National Park, 23 July 1994; 7 ♀♀, pool at Twin Falls, Kakadu National Park, 23 July 1994; 2 ♀♀, pool near Jim Jim Falls, Kakadu National Park, 23 July 1994; 2 ♀♀, plunge pool at Barramundie Creek, Kakadu National Park, 24 July 1994; 5 ♂♂, 20 ♀♀, plunge pool at Gunlom Falls, Kakadu National Park, 25 July 1994; 1 ♂, Lily Ponds Falls, Katherine Gorge National Park, 27 July 1994; 1 ♂, 10 ♀♀, plunge pool at Edith Falls, Katherine Gorge National Park, 30 July 1994.

WESTERN AUSTRALIA. ZMA, 1 ♀, pond at Dales Gorge, Hamersley Range National Park, 12 August 1994; 1 ♂, pond at Kalamina Gorge, near falls, Hamersley Range National Park, 13 August 1994; 1 ♂, Python Pool, Millstream-Chichester National Park, 17 August 1994.

Remarks. The species has previously only been reported from Northern Territory. The new records from Western Australia mean a considerable range extension of the species.

According to Harvey (1988b), the PIV has a small, thickened seta on the medial side. However, in the majority of specimens from this study, this seta is lacking in both males and females.

***Pseudohydryphantes mataranka*
Harvey, 1988**

Pseudohydryphantes mataranka Harvey, 1988b: 24.

Material examined. NORTHERN TERRITORY. ZMA, 1 ♂, Baboalba Springs (Gubarra), Kakadu National Park, 20 July 1994; 1 ♂, pool at Twin Falls, Kakadu National Park, 23 July 1994; 1 ♂, 1 ♀, plunge pool at Gunlom Falls, Kakadu National Park, 25 July 1994; 2 ♂♂, Lily Ponds Falls, Katherine Gorge National Park, 27 July 1994; 2 ♂♂, plunge pool at Edith Falls, Katherine Gorge National Park, 30 July 1994.

WESTERN AUSTRALIA. ZMA, 1 ♂, 2 ♀♀, Forteseue Falls (pool), Hamersley Range National Park, 11 August 1994; 1 ♀, Circular Pool, Hamersley Range National Park, 12 August 1994; 1 ♀, pond at Dales Gorge, Hamersley Range National Park, 12 August 1994; 3 ♂♂, 3 ♀♀, pond at Kalamina Gorge, near falls, Hamersley Range National Park, 13 August 1994; 1 ♀, Palm Pool, Millstream-Chichester National Park, 15 August 1994; 1 ♀, Crossing Pool, Millstream-Chichester National Park, 16 August 1994; 1 ♂, 1 ♀, pond at Snake Creek, Millstream-Chichester National Park, 17 August 1994; 2 ♀♀, Python Pool, Millstream-Chichester National Park, 17 August 1996; 1 ♀, Forteseue River at crossing with North West Coastal Highway, 18 August 1994.

Remarks. Previously, the species has only been reported from Northern Territory (Harvey 1988b). The new records from Western Australia mean a considerable range extension of the species.

***Pseudohydryphantes gracilipalpis* sp. nov.
(Fig. 1A-E)**

Type material. HOLOTYPE - NTM I-678, ♂, plunge pool at Edith Falls, Katherine Gorge National Park, Northern Territory, Australia, 30 July 1994. PARATYPES - ZMA, 2 ♀♀; NTM I-681, I-682, 2 ♀♀, same data as holotype.

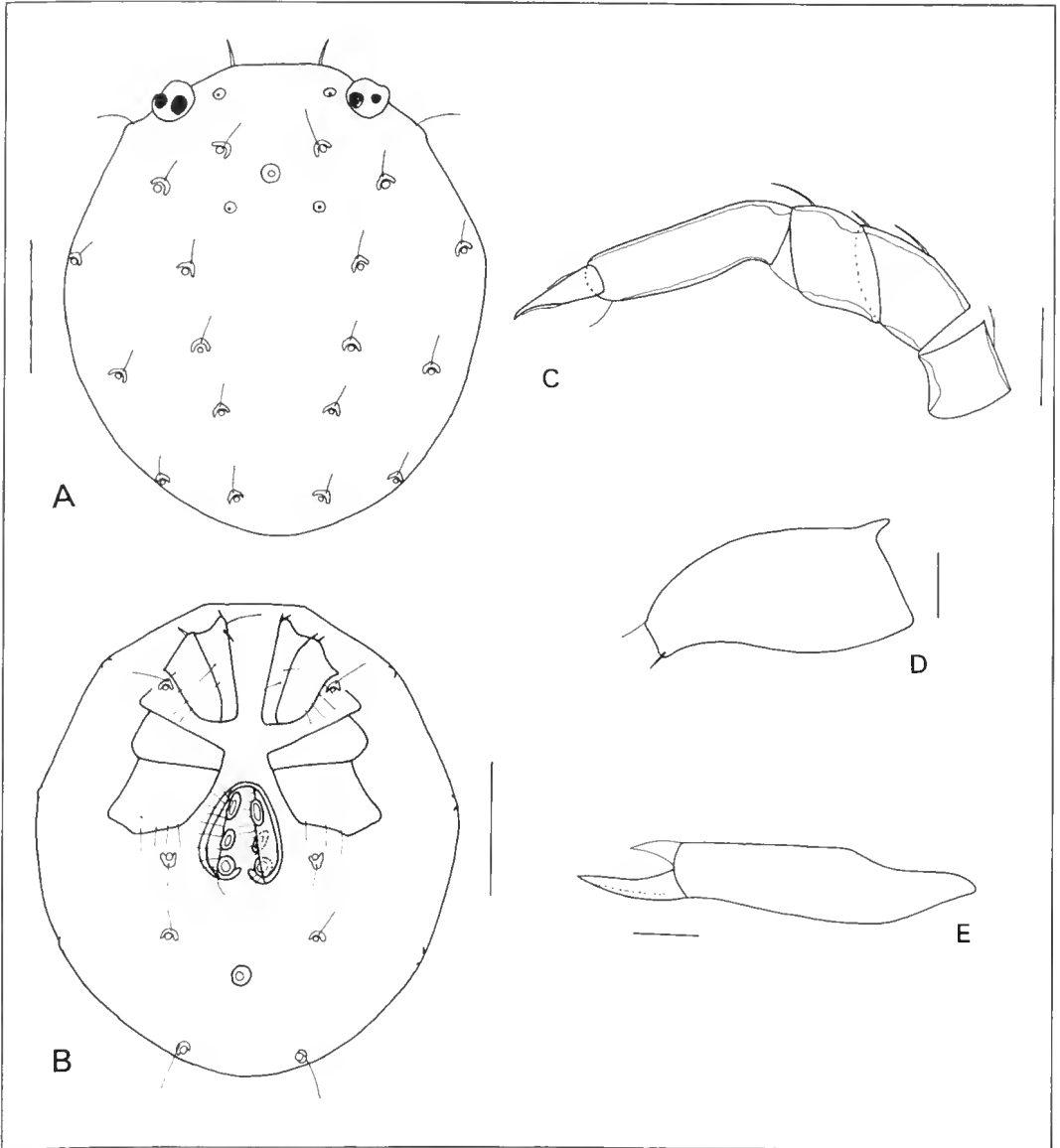


Fig. 1. *Pseudohydryphantus gracilipalpis* sp. nov., holotype ♂: **A**, dorsal view; **B**, ventral view; **C**, palp; **D**, capitulum; **E**, chelicere. Scale bars: A and B 200 µm; C-E, 50 µm.

Diagnosis. The PIV lacking an anterodorsal extension and the very slender PV are diagnostic for the new species.

Description. Male. Body 701 long and 621 wide. Integument papillate. Lateral eyes on ocular tubercles. Sclerites associated with glandularia crescent shaped. Median eye on same level as dg3, postocularia posteriorly of dg3 (Fig. 1A). Capitulum without long, downturned anterior extension (Fig. 1D).

Chelicera of normal shape, 250 long; cheliceral claw curved, with 14-15 teeth, cheliceral lamella slightly bowed (Fig. 1E). Genital field 144 long. Three pairs of acetabula, the posterior pair ovoid, the two anterior pairs elongate. Mesial edge of genital flaps with a row of long setae (Fig. 1B). Excretory pore surrounded by sclerotization. Vg3 anterior to excretory pore, vg4 situated laterally. Dorsal lengths of

PI-PV: 38, 70, 37, 108, 49. PIV without anterodorsal extension and without seta on medial side, PV very slender (Fig. 1C). Dorsal lengths of I-leg-4-6: 82, 108, 130; dorsal lengths of IV-leg-4-6: 137, 144, 125. Third and fourth legs with swimming setae: III-leg-3 with one to two, III-leg-4 with seven, III-leg-5 with eight, IV-leg-3 with one to two, IV-leg-4 with four to seven and IV-leg-5 with eight. Claws without serration or teeth.

Female. Body 747-786 long and 621-669 wide. Location of glandularia as in male. Chelicera 245 long, shape as in male. Genital field 185 long, the posterior pair ovoid, the two anterior pairs elongate. Mesial edge of genital flaps with a row of long setae. Excretory pore surrounded by sclerotization. Lengths of PI-PV: 38, 72, 38, 108, 48; palp as in male. Lengths of I-leg-4-6: 91, 113, 128. Lengths of IV-leg-4-6: 142, 152, 130. Third and fourth legs with swimming setae: III-leg-3 with one, III-leg-4 with five, III-leg-6 with six, IV-leg-3 with one, IV-leg-4 with five and IV-leg-5 with six. Claws without serration or teeth.

Remarks. The new species has a very unusual palp. The PIV is lacking an anterodorsal extension, a character not found in any other member of the genus. This character is very rare in the family Hydryphantidae (Cook 1974).

Etymology. Named for its very slender PV.

Pseudohydryphantes elongatus sp. nov.

(Fig. 2A-E)

Type material. HOLOTYPE - NTM 1-679, ♂, pool at Twin Falls, Kakadu National Park, Northern Territory, Australia, 23 July 1994.

Diagnosis. Sclerites associated with glandularia crescent shaped. Dg1, lg1 and lg2 large. Median eye slightly anterior of dg2. Postocularia on same level as dg3, relative far posterior of median eye.

Description. **Male.** Body elongated, 553 long and 364 wide. Integument papillate. Lateral eyes on ocular tubercles. Sclerites associated with glandularia crescent shaped. Crescents relative short and broad. Dg1, lg1

and lg2 large. Median eye slightly anterior to dg2. Postocularia on same level as dg3, relatively distant posterior to median eye (Fig. 2A). First coxae with small, blade-like setae. Capitulum very short, without long, downturned anterior extension (Fig. 2D). Chelicera of normal shape, 245 long; cheliceral claw curved, with approximately 10 teeth, cheliceral lamella almost straight (Fig. 2E). Genital field 151 long. Three pairs of acetabula, the posterior pair ovoid, the two anterior pairs elongate. Mesial edge of genital flaps with a row of long setae (Fig. 2B). Excretory pore surrounded by sclerotization. Lengths of PI-PV: 41, 84, 47, 122, 29; PIV with a small seta on ventral side (Fig. 2C). Lengths of I-leg-4-6: 94, 106, 125. Lengths of IV-leg-4-6: 146, 156, 122. Third and fourth legs with swimming setae: III-leg-3 and IV-leg-3 with one, III-leg-4 with five, III-leg-5 with seven, IV-leg-4 with six and IV-leg-5 with five. Claws without serration or teeth.

Female. Unknown.

Remarks. The new species is close to *P. crassipes* Cook, *P. cooki* Harvey and *P. aroona* Harvey. It differs from these species in the configuration of median eye, postocularia and dg2 and dg3. Moreover, the sclerites of *P. crassipes* are small and not crescent shaped, the excretory pore of *P. cooki* is not completely surrounded by sclerotization, and the pre- and postocularia and median eye of *P. aroona* have much larger sclerotization.

Etymology. Named for the slender body shape.

Cyclohydryphantes Lundblad, 1941

Cyclohydryphantes Lundblad, 1941: 111.

The genus *Cyclohydryphantes* is endemic to Australia. So far, two species have been described, i.e. *C. trabeculiferus* Lundblad, known from Victoria and Tasmania, and *C. unutarnee* Harvey from Queensland.

Cyclohydryphantes occidentalis sp. nov.

(Fig. 3A-F)

Type material. HOLOTYPE - WAM 98/1588, ♀, Circular Pool, Hamersley Range National Park, Western Australia, Australia,

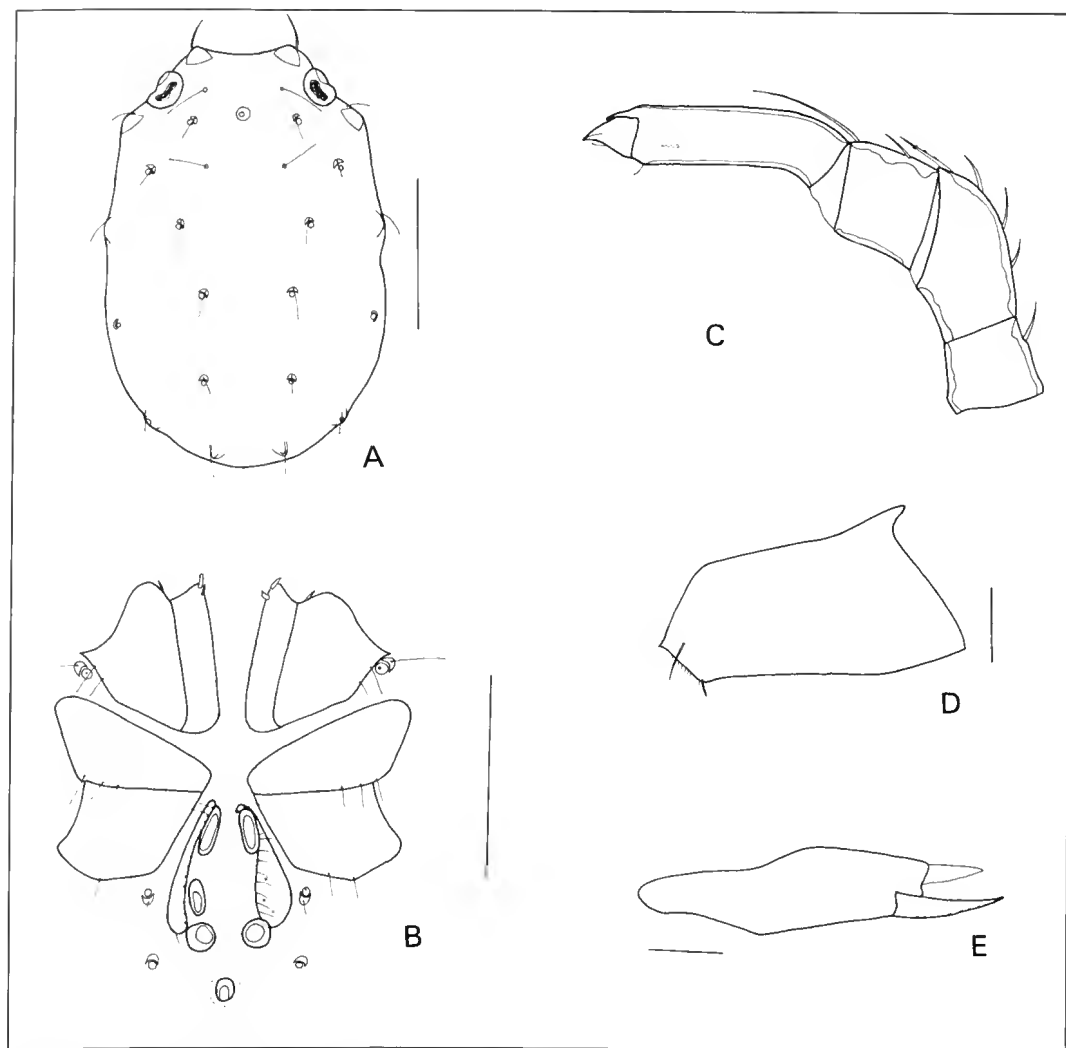


Fig. 2. *Pseudohydryphantus elongatus* sp. nov., holotype ♂: A, dorsal view; B, ventral view; C, palp; D, capitulum; E, chelicere. Scale bars: A and B, 200 µm; C-E, 50 µm.

12 August 1994. PARATYPES - WAM 98/1589, 1♀, same data as holotype; ZMA, 2♀♀; NTM I-680, 1♀, pool at Joffre Gorge, Hamersley Range National Park, 13 August 1994.

Diagnosis. Preocularia rounded, antenniform plate with short branches, *lg1* elongated, sclerites associated with ventroglandularia crescent shaped.

Description. *Female.* Body 1072 (1128-1176) long and 902 (980-1004) wide. Integument papillate. Lateral eyes on ocular tubercles. Sclerites associated with *dg4*, *dg5*, *dg6*, *vg2* and *vg2* crescent shaped, *vg1* with a ring-shaped sclerite, all other glandularia

on elongate platelets (Fig. 3A). Preocularia rounded, antenniform plate with short branches (Fig. 3C). Genital field 208 long. Genital flaps with a mesial row of long setae. Three pairs of acetabula, the posterior pair rounded, the two anterior pairs elliptical (Fig. 3B). Capitulum short, anteriorly short downturned (Fig. 3E). Chelicera of normal shape, 359 long; cheliceral claw slightly curved, with approximately 12 small teeth, cheliceral lamellae pointed (Fig. 3F). Lengths of PI-PV: 50, 96, 61, 155, 36; PII with two long seta on medial side, PIV with a short seta distally on medial side (Fig. 3D). Lengths of I-leg-4-6: 126, 131, 126; lengths

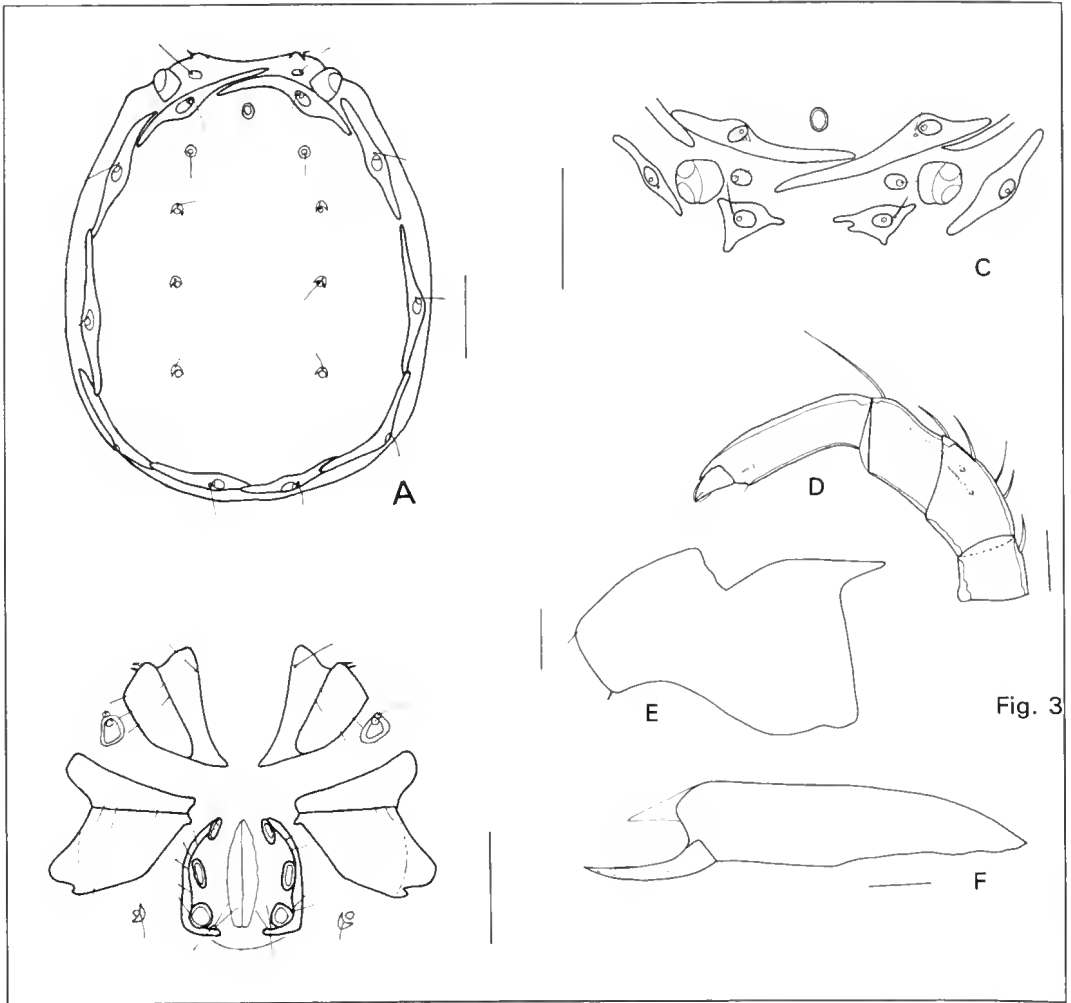


Fig. 3. *Cyclohydriphantes occidentalis* sp. nov., holotype &: **A**, dorsal view; **B**, ventral view; **C**, anteromedial view; **D**, palp; **E**, capitulum; **F**, chelicere. Scale bars: A-C, 200 µm; D-F, 50 µm.

of IV-leg-4-6: 213, 233, 126. Third and fourth legs with swimming setae: III-leg-3 with one to two, III-leg-4 with five to six, III-leg-5 with six to seven, IV-leg-3 with one, IV-leg-4 with eight and IV-leg-5 with six to seven. Excretory pore surrounded by sclerotization.

Male: Unknown.

Remarks. The new species is close to *Cyclohydriphantes trabeculiferus* Lundblad, but differs in the shape of preocularia (triangular in *trabeculiferus*), the shape of the antenniform platelet (*C. trabeculiferus* has long branches), the shape of the sclerite of lg1 (shorter in *C. trabeculiferus*). Furthermore, the sclerites of vg2 and vg3 of *C. trabeculiferus* are

rounded. *Cyclohydriphantes trabeculiferus* (1405-1930 long) is much larger than the new species.

Etymology. The name of the new species refers to its occurrence in Western Australia.

Diplodontus Dugès, 1834

Diplodontus Dugès, 1834: 17.

Diplodontus haliki Lundblad, 1947

Diplodontus haliki Lundblad, 1947: 30.

Diplodontus haliki - Cook 1986: 18; - Smit 1992: 93.

Material examined. *Western Australia.* ZMA, 1♂, western part of Deep Reach Pool, Millstream-Chichester National Park, 16 August 1994.

Remarks. The species has been reported from Victoria, New South Wales and Tasmania. The new record from Western Australia means a considerable range extension of the species.

ACKNOWLEDGMENTS

I am indebted to the Western Australian Department of Conservation and Land Management (Como), the Australian National Parks and Wildlife Service (Darwin) and the Conservation Commission of the Northern Territory (Palmerston) for their permission to collect water mites in the national parks of Western Australia and Northern Territory and to G.M. van der Pal for her assistance with the fieldwork.

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Accepted 9 June, 1998

A ROCK PAINTING, POSSIBLY OF THE NOW EXTINCT
MARSUPIAL *THYLACOLEO* (MARSUPIAL LION),
FROM THE NORTH KIMBERLEY, WESTERN AUSTRALIA

KIM AKERMAN

*Museum and Art Gallery of the Northern Territory,
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ABSTRACT

A painting of a large quadruped from the Irregular Infill (Large Naturalistic) rock art period of the Kimberley is discussed in terms of the possible identity of the subject. Morphological features such as the overall shape and body proportions, in particular the leg/body ratios, are examined in order to minimise possible ambiguities in the allocation of a specific identity to the animal depicted. While some features such as the absence of the large thumb and claw on the forelimbs may mitigate against the identification, it is suggested that the painting may be a depiction of the extinct marsupial lion *Thylacoleo carnifex*.

KEY WORDS: rock art, Irregular Infill (Large Naturalistic) Period, extinct fauna, *Thylacoleo*, Kimberley, Western Australia

INTRODUCTION

In 1983 during ethnographic reconnaissance along the lower reaches of the King George River and the adjacent north Kimberley coast, I located and briefly examined several rock shelters, close to each other and adjacent to the river, that had apparently been painted at different periods of time. While some paintings were in the recent Wandjina style, depicting anthropomorphs, yams and animals, including a life-size sea turtle and fish, most of the other paintings fell into that category generally known as Bradshaw Figures. Bradshaw paintings are regarded as belonging to a much earlier period than the Wandjina and other art styles created in the recent traditional past. Walsh (1994: 18) and Welch (1993: 99–113) have each provided a model of the Kimberley rock art sequence. Walsh's model is extremely detailed, perhaps over complex, while that provided by Welch is much more conservative. Both models incorporate an early Archaic phase, an intermediate phase that includes the period when Bradshaw art was produced and a recent phase that continued into the ethnographic present merging into the period of European contact and settlement. It is evident, however, that both models are

relevant to the north-western, central and northern Kimberley rather than the southern or eastern sections of that region.

In July 1990, while again conducting surveys in the same area, I was directed by the traditional custodian of the area, Mr Vernon Gerard, to a superb frieze of very large Bradshaw Figures painted on a rock face adjacent to the river and about one kilometre from the shelters I had examined seven years earlier. Some of the figures are over a metre tall, and although totally exposed to the elements, are in an excellent state of preservation.

It was clear that the area deserved further investigation and in an hour I located more than a dozen overhangs or shelters decorated with a wealth of rock art. A wide array of Bradshaw Figures ranging from the very simple to the extremely ornate and of all dimensions were to be found throughout the area. One large wall was filled with life-sized, naturalistic paintings of macropods. Other shelters held archaic bichrome paintings of human figures with boomerangs. Only in two shelters were there paintings that could be considered as belonging to the most recent rock art phase—the turtle shelter that I saw first in 1983 and another, with paintings that

included a polychrome snake, a large kangaroo and a slender Wandjina-like image with the lower left leg twisted outwards at the knee.

As striking as the elegant Bradshaw Figures were, the image that caught my attention was that of a large ($L = 1$ metre), solitary leaping animal painted on the wall of an outcrop at the southern extremity of the general gallery area (Fig. 1). The image was old and the ochre with which it had been originally painted was skillfully applied to the very exposed rock wall. It appeared to be of the same stylistic genre as the panel of large naturalistic macropods referred to earlier. The macropods belonged to that art period designated by Walsh (1994: 35), as the Irregular Infill Animal Period (IIAP) of the Archaic Epoch which, on the basis of superimposition, is generally believed to have been created at an earlier period than the Bradshaw paintings.

Paintings from the Irregular Infill Animal Period of the Kimberley appear to be similar

in style to those belonging to Chaloupka's Large Naturalistic phase (LNP) of rock art from western Arnhem Land. Animals painted in both the Irregular Infill Animal Period and the Large Naturalistic style are depicted life-sized and usually very true to form in the case of recognisable species. Images of kangaroos and wallabies have been recognised in the Kimberley IIAP, and are common in the LNP of Arnhem Land along with large pythons (*Morelia oenpelliensis*), rock possums (*Pseudocheirus dahli*), Tasmanian devils (*Sarcophilus harrisii*) and Tasmanian tigers (*Thylacinus cynocephalus*). Ancient extinct forms that have been recognised include the giant echidna (*Zaglossus*), marsupial lion (*Thylacoleo carnifex*), the marsupial tapir (*Palorchestes*) and single-toed kangaroos (*Sthenurus*) (Murray and Chaloupka 1984: 105–116; Chaloupka 1993: 93).

The profile of these animals is usually depicted naturalistically with head and extremities usually presented in solid colour.

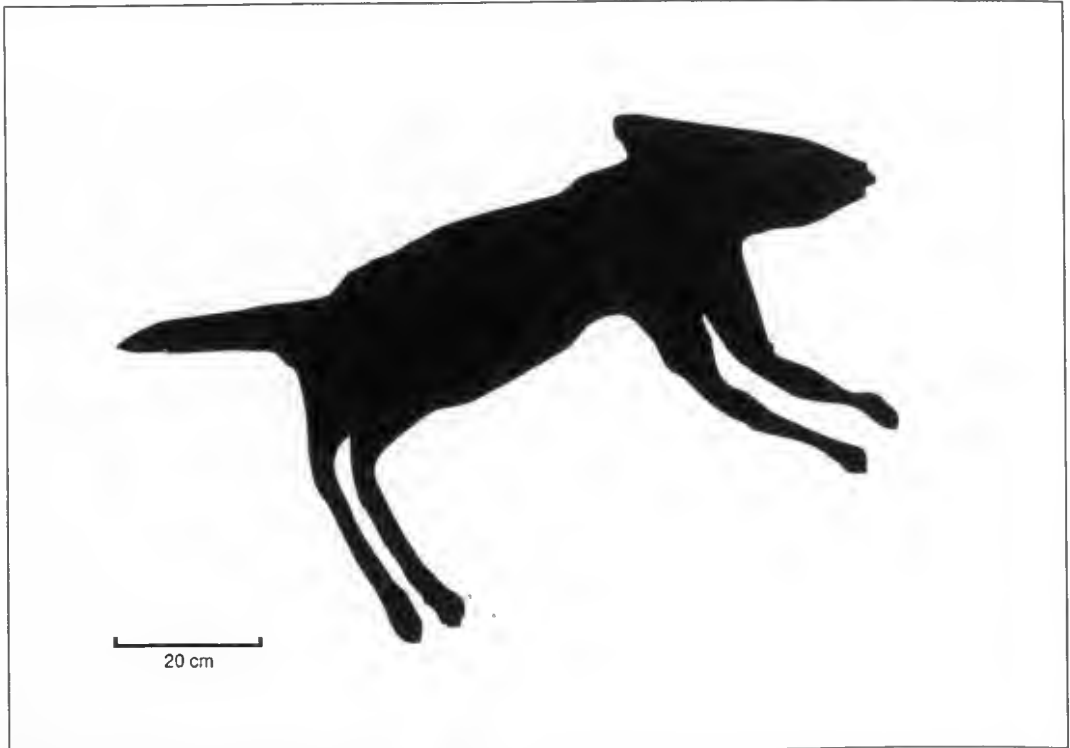


Fig 1. Figure of a leaping quadruped, possibly a *Thylacoleo*, drawn from computer enhanced 35 mm transparency of a rock painting located in the vicinity of the lower King George River, Kimberley, Western Australia.

The rest of the body area may be infilled either with solid colour or with a range of irregularly applied dots, dashes, or random lines of pigment.

Figure 1 traced from a transparency of the painting shows a cat-like animal with short, thick, stiffly-pointed tail. The body, relatively short between hip and shoulder, is placed between extended rear and fore-quarters and a frontally flattened head with large, pointed, laid back ears. The hind legs are extended back from the body then swung forward and under it as if the animal is praneing or leaping up, an attitude reinforced by the alignment of the posture of the head on the shortened neck, pulled into the shoulders, and emphasised by the ears that follow the profile of the skull. The awkwardly curved rear legs could suggest that the beast has a long tarsal section, but I believe that the legs are drawn in this manner to emphasise the movement rather than an anatomical reality. The long, muscular forelegs are raised as if batting at an object, rather than grasping or clawing at something. The extremities of both hind and fore-limbs end in well-defined paws, with the fore-limbs suggesting a flexibility of movement in the wrist. In contrast to the hind limbs, those in front have well-defined musculature and movement that suggests they exhibit a strength and agility that may have been considered a characteristic of the beast portrayed.

Identification of faunal images, particularly extinct forms, in rock art is fraught with difficulty and, in the past, such identifications have created some interesting debate (Basedow 1914: 200–203; Mountford 1929: 243–248; Hall *et al.* 1951: 375–380; Tindale 1951: 381–382; Calaby and Lewis 1977: 150–151; Brandl 1980: 6–13; Murray and Chaloupka 1984: 105–116; Lewis 1986: 140–145; Chaloupka and Murray 1986: 145–147; Berndt 1987: 15–28). The rock surface on which the animal was painted was exposed to the elements and there was no evidence of other paintings or superimposition that could create a misleading composite image and an ill-founded identification. Examination of the literature pertinent to large marsupials, both extinct and extant, allows me, I believe, to

maintain my initial field identification that the animal depicted in this singular painting was in all probability a marsupial lion, *Thylacoleo carnifex*.

The style of the painting, placing it within the Irregular Infill Animal Period, in which paintings appear to be of a 1:1 scale with their subjects, suggests that the animal itself was of similar dimensions. The legs of equal length suggest either a dog-like or cat-like animal, possibly either a *Thylacine* or a *Thylacoleo*. Lack of stripes on the hind quarters, generally accepted as a distinguishing mark when identifying prehistoric images of the former animal, coupled with a stiff or erect tail, mitigate against the image being that of a *Thylacine*. Walsh (1994: 284–285) illustrates a painting from the Kimberley, identified as a *Thylacine*, that shows striped rump and tail with the rest of the animal infilled with solid colour. The decidedly thickened base of the tail would seem to indicate that the image is meant to be of a marsupial, rather than a placental animal such as a dog. Prehistoric images of *Thylacine* elsewhere in Australia also usually show the animal with dog-like heads of relatively large size. Palaeontological reconstructions (Murray and Chaloupka 1984: 111) of *Thylacoleo* on the other hand have rounded, more feline heads, with broader muzzles. Murray (Murray 1984: 16, 18, 26–27; Murray and Chaloupka 1984: 111) recreated *Thylacoleo* as a robust animal, as did Schouten (Quirk and Archer 1983: 53). Knight (Rich and van Tets 1985: 229), on the other hand, produced a more gracile animal. In terms of size and conformation, *Thylacoleo* is often compared in the literature with a leopard (Finch 1971: 10; Quirk and Archer 1983: 52). Tentative identifications of *Thylacoleo* images in the rock art of Arnhem Land have been made by Murray and Chaloupka (1984: 111–112). Chaloupka (pers. comm.) has recently photographed two more images of the same animal that are painted on the walls of shelters in central Arnhem Land.

The posture of the animal in the Kimberley painting, as described above, suggests that it is leaping up with the well-defined fore-legs clearly matching the hind limbs in length. As Finch (1971: 9) notes,

Thylacoleo fore and hind limbs lengths are approximately equal. Finch (1971: 8) also draws attention to the fact that, when compared with the length of the vertebral column, it is clear that *Thylacoleo* has a very long forelimb for its body size with a forelimb/vertebral column ratio of about 3:4. Finch also demonstrates that *Sarcophilus*, like *Thylacoleo*, has a very long forelimb in proportion to its body length, a feature that is usually omitted in images of the former animal. As Calaby and Lewis (1977: 150) point out, devils are recognised in rock art by their stout bodies, short legs and broad blunt heads with short rounded ears. The squat, solid image usually presented of *Sarcophilus* is related to its posture and thick pelage rather than actual body structure. On the basis of the relative limb size I am inclined against the possibility that the Kimberley painting may be of a Tasmanian devil (*Sarcophilus*).

Two of the most distinctive features of *Thylacoleo* remains are not indicated on the painting. The first are the massive premolars with their long shearing edges, which would only be visible if the animal was open-mouthed and consequently not an issue when discussing this image. The second is more problematical and that is the absence of the extremely large claws that arm the very mobile pseudo-opposable thumbs. The thumb and other phalanges bear sheathing bases at their tips, indicating that the claws that armed them were retractible in the same way as those of most cats. If the animal is indeed a *Thylacoleo*, the absence of the large thumb claw may possibly be explained by the closed-paw batting action that appears to be depicted, ensuring that thumb was held close to the body of the manus and not prominent as it would be if the paws were spread or extended.

At the muzzle of the large head with flattened forehead and laid-back ears a faint protrusion may indicate the upper lip or tongue, or possibly the strong, caniniform incisors unique to *Thylacoleo* (Wells *et al.* 1982: 577). The lower incisors possess serrated ridges and are designed for stabbing, while the upper incisors hold the prey against the lower teeth. The upper incisors also serve as whet stones against which the lower incisors are honed, much as

a wild boar uses its upper canines to maintain the tusks that are set in the lower jaw. The jaws and incisors may also operate in a pincer movement to strangle smaller prey in much the same way as a lion or leopard kills. It is believed that the long, strong arms may have been used to subdue and grasp prey animals that were then strangled by biting across the neck. The sabretooth tiger (*Smilodon fatalis*) possessed similar robust forequarters that, it is believed, were also used to hold prey which were killed by repeated stabbing with the massive canines (Stock 1992: 32–34).

According to Wells (1985: 228), *Thylacoleo* ranged throughout Pleistocene Australia, becoming extinct during the last great glacial maximum at about 18,000 BP. If the Kimberley painting is indeed a representation of *Thylacoleo*, an early date can be assigned to it and also possibly to other large naturalistic paintings executed in the same genre. Such a date would not be entirely out of place with the 17,000 BP minimum date, derived from fossil mud-wasp nests, assigned to a north Kimberley Bradshaw-like painting (Roberts *et al.* 1997: 696–699). The art sequence for the north Kimberley, as recognised by Walsh (1994: 18), places large naturalistic animals within the Irregular Infill Animal Period of the Archaic Epoch which precedes the Erudite Epoch, within which Bradshaw art is located.

Wells (1985: 228) postulates that as a dominant predator, *Thylacoleo* would have been thinly distributed over its range, a situation reflected in its generally infrequent presence in the fossil record. Aboriginal representations of extinct fauna such as this image allow the distribution of a particular faunal species to be extended beyond a range solely derived from palaeontological evidence. Such images, perhaps even more importantly, serve as vital reflections of the changing natural environment within which Aboriginal society has existed for the past 50,000 years.

ACKNOWLEDGMENTS

I wish to thank Vernon Gerard who drew my attention to rock art of the King George River area and gave me permission to record

the same. I am also most grateful to George Chaloupka (Museum and Art Gallery of the Northern Territory) and Dr David Welch (Darwin), who have provided most useful comments and criticism of the draft manuscript. Over the years Peter Murray and Dirk Megirian, both of the Museum and Art Gallery of the Northern Territory, have generously given access to their vast body of information relating to the extinct faunal assemblages of Australia. Finally I wish to thank Steve Carrol of the Graphics section, Museum and Art Gallery of the Northern Territory, for producing the image used to illustrate this paper.

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Accepted 10 March, 1998

THE *PELÉDANG*. THE LASHED-LUG WHALING CRAFT OF LAMALERA, LOMBLÉN (LEMBATA), NUSA TENGGARA TIMUR, INDONESIA

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ABSTRACT

The men of the village of Lamalera, situated at the mouth of Lebala (Labala) bay on the south coast of the island of Lomblén (Lembata), must be among the last of the traditional maritime big game hunters. Conservative in their technology, they go to sea in hand built lashed-lug watercraft, propelled by paddles and woven palm-leaf sails to take giant manta ray, ocean sun-fish, leatherback turtle, shark, dolphin and other small toothed whales, and sperm whale, with hand forged harpoons and lines of cotton or lontar palm and hibiscus fibre. Their catch is either consumed locally or exchanged at adjacent markets for goods they cannot produce themselves, particularly cotton, tobacco, maize, cassava, fruit and other vegetables. A description of their lashed-lug boat, the *pelédang*, and associated technology is provided, along with other brief notes on the division of game.

KEYWORDS: Lashed-lug watercraft, maritime hunting, Lamalera, Indonesia, *pelédang*, whaling

INTRODUCTION

The villagers of Lamalera (Lamalera), on Lebala bay, south coast of the island of Lomblén, Indonesia (Figs 1–2) are believed to have followed a maritime economy based on the hunting of large sea creatures including sperm whales for well over two hundred years (Barnes 1980: 6). The hunters of Lamalera pursue their prey in large lash-lugged boats known as *pelédang* (sometimes written *pledang* or *pelendang*) or *téna*. Apart from the work of R.H. Barnes and a major study of Lamalera *ikat* fabrics by Ruth Barnes (1989), documentation of the people and economy of the people of Lamalera has generally been limited to articles in popular magazines promoting tourism (eg. Fuchs 1984: 22–27; Masyhur 1987: 32–39; Moore 1995: 100–112). Barnes presents, in a series of papers, a history of Lamalera, its economy and technology (Barnes 1974: 137–159; 1980: 1–82; 1984: 1–32; 1985: 345–366). This work was brought together and extended in a most comprehensive and detailed study in *Sea Hunters of Indonesia* (Barnes 1996). Barnes (1984) provides a description of the impact of introduced

modern technology, in the form of a motorised whale chaser, on the community of Lamalera. This work should be mandatory reading for any individual or organisation involved with the introduction of technological change in traditional societies. Horridge (1982: 49–55) deals with some aspects of the construction of the Lamalera craft in his seminal work on the lash-lugged boats of Eastern Indonesia and the Philippines.

Our own interest is two-fold. Dwyer has maintained a long-term interest in the watercraft of the Indonesian Archipelago; while Akerman, having concentrated on the material culture of Australian Aboriginal people, was interested in observing that of a maritime hunting people. Our specific interest in the unique situation that existed at Lamalera was further whetted on viewing the televised documentary *Whale hunters of Lamalera* (Granada Television 1988), a production for which Barnes had served as anthropologist. It was clear, on viewing this footage, that the people of Lamalera retained a far more traditional approach to both their watercraft technology and their economy than that other notable group of maritime

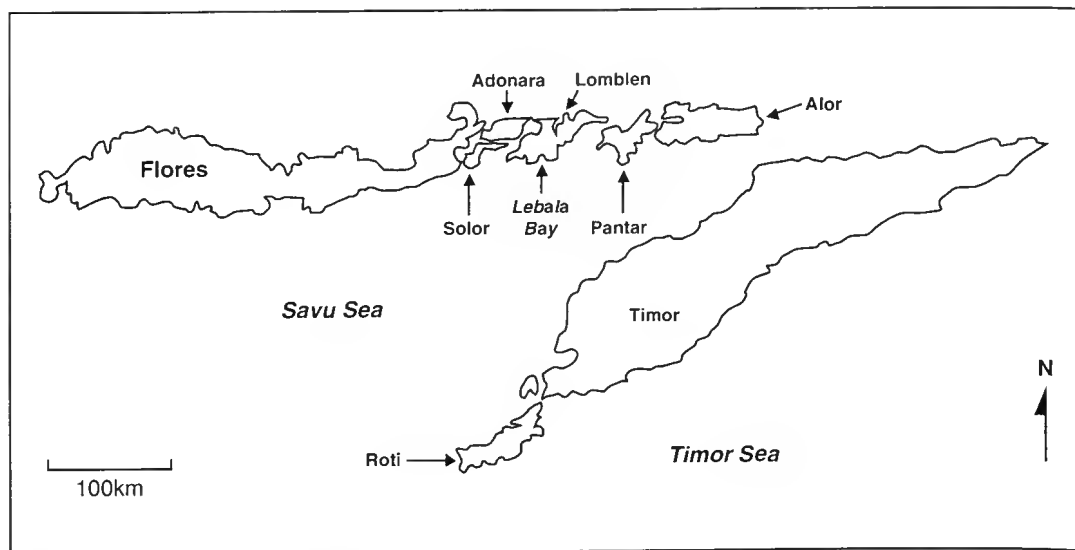


Fig. 1. Savu Sea showing the position of the island of Lomblen.

hunters, the Inuit of the northern polar regions.

In August 1993 we travelled to Lamalera carrying letters from a colleague at the Museum and Art Gallery of the Northern Territory to Josephus Bataona, head of the Bataona clan. Josephus not only offered us a place to stay within his household, but also arranged for us to sail with the crew of the *Holo Sapang* and inventory and take the lines and other details of the vessel *Sili Téna*. The latter boat had been extensively rebuilt prior to our visit and lay outfitted, but temporarily crewless, in its boatshed or *naje*. It was not our intention to carry out formal fieldwork at Lamalera and the following notes are derived from our diaries.

As Barnes's writings provide detailed descriptions of much of the boat and hunting technology from an ethnographic perspective, our aim here is to present the lines of a *pelédang* and provide technical data about the craft and the manner in which they are operated. Illustrations provided by Barnes are very schematic and it was our intention to recast the technical details of the *pelédang* with attention to the relevant proportions. It was also clear after sailing in the *Holo Sapang*, that comments made by Horridge (1982), particularly in relation to the effectiveness of the rigging and sailing capabilities of the *pelédang*, were

inadequate. We also noted details of butchering patterns of a number of species of marine animals (Appendix 1). Although we did not see a whale taken and butchered, details of the division of a whale were provided by Josephus Bataona. A sketch map of the beach showing landing points and the disposition of the boatsheds and an inventory of the craft was also made. Each evening we spent time going over the day's work with Josephus, who would correct and guide our investigations. All conversations were conducted in Bahasa Indonesia, which Dwyer spoke with proficiency, rather than in the indigenous Lamaholot spoken by Lamalerans.

Neither of us possess the ear of a trained linguist so we have recorded and transcribed Lamaleran terms as we believe we heard them. Apart from two diacriticals (é, â), we have adopted standard Indonesian orthography in the transcription of words. It must be pointed out that a final 'ng' sound on a word, occurring after the vowel 'a', seems to be an unvoiced alveopalatal nasal rather than the voiced alveopalatal nasal that occurs, for instance, in the English pronunciation of the word -rang, that is 'ang' presents, in Lamaleran, as a much softer, almost silent sound. Where we believe it occurs in a word we show it thus: â.

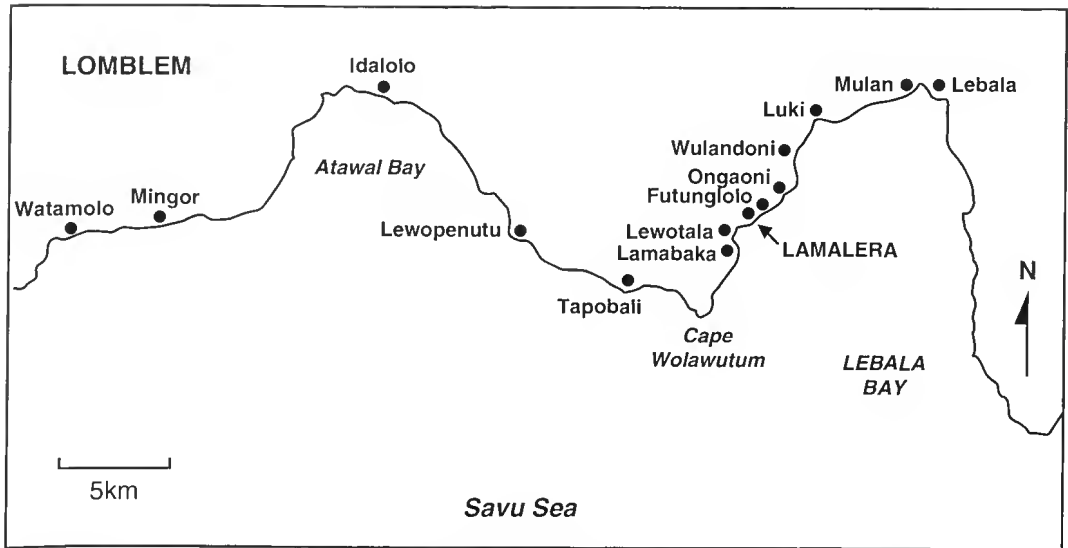


Fig. 2. Lebala Bay, Lomblen, showing Lamalera and adjacent population centers. Taken from a tourist map produced at Lewoleba, Lomblen.

GENERAL DISCUSSION

Generally, the lashed-lug plank boats of southeast Asia are watercraft built of edge-dowelled planks that have projecting cleats or lugs on them that are pierced to take lashings that bind them to thwarts and ribs. Manguin (1985: 334–335) intimates that lashed-lug craft were preceded by and developed from sewn-plank vessels. Manguin presents the 3rd Century AD Pontian wreck from the east coast of the Malay Peninsula as an example of the transition between sewn-plank and lashed-lug craft. The Pontian boat possesses edge-dowelled planks and lugs pierced for lashings in addition to aligned holes in adjacent planks that indicate they were also sewn together. Lashed-lug boats from Europe, including those from the early Viking period, were clinker built, with overlapping planking rather than edge-fitted with each plank flush with the next. Horridge (1982: 1) believed that watercraft built on lashed-lug principles had been employed for at least a thousand years in the Indo-Pacific region. Recent archaeological evidence provides even greater antiquity with the recovery of lashed-lug boats dated between AD 320 and AD 1250 from excavations conducted along the Masao

River on Mindanao (Abinon 1989: 1–2; Clark *et al.* 1993: 143–159; Green *et al.* 1995: 177–188; N. Burningham, written comm.).

The hull construction of lashed-lug plank boats has been broken into the following components by Horridge (1982: 1) :

- a) the shell-first construction on a keel or dug-out foundation;
- b) edge-dowelled planking of hardwood carved to shape;
- c) lugs carved *in situ* in transverse rows across the inside of the boat;
- d) flexible frames placed in tension to compress the planks together;
- e) many transverse thwarts also lashed down to the lugs and rib-ends to squeeze the hull.

While we have no general problem with these conditions we believe that Horridge may be overly precise on some points. For example, we found that the ribs, far from being flexible, were in fact quite solid. This point is also made quite explicitly by Barnes (1985: 359). It was the flexible dowelled planking that was pulled to the ribs as they were being lashed into place. The result is not a rigid pre-stressed structure as implied by Horridge (1982: 59), but a flexible pre-

stressed structure. Rather than focussing on other aspects of Lamaleran boat construction *vis a vis* Horridge's work, we provide details of what we observed in our brief visit to the village.

THE HULL OF THE *PELÉDANG*

For many highly important anthropological details on the actual method of construction of the *pelédang*, and the social significance both of its parts and as a whole, the reader is urged to read Barnes's publications of 1974 and 1985.

We commenced our study of the *pelédang* by lifting the lines following directions provided by Leather (1989: 29–33). Measurements were made in imperial units which were then converted to metric. The Sili Téna was worked on where it lay in its shed and we were unable to ensure that it was completely level. Some fairing was made when drawing up the lines to compensate for errors of measurement that may have occurred (Fig. 3). Scope remains for more accurate drawings to be made in the future. Having said that, the lines produced, we believe, reflect accurately the shape of the hull and show a very different watercraft than might be envisaged from the schematic drawings provided by Barnes (1985: 348–350). With a length-to-beam ratio of 5:1 and simple doubled ended shape, the craft conforms to the general shape of whale boats that have been developed in other parts of the world (Chapelle 1951: 41–42; Whipple 1979: 94).

Pelédang must be as light as possible yet robust. Each day they are manhandled from the boat sheds to the sea and back. They must be capable of being paddled in pursuit of their quarry and strong enough to withstand the buffeting of flailing tails and powerful manta ray wings. As well as ensuring speed when in pursuit of game, the slim lines and the length at waterline give the boat sufficient hull speed to minimise the likelihood of sinking by the stern when towed by a harpooned whale.

The keel (*iye*) and the planks making up the five lower strakes (*arā*) all have a series of aligned carved lugs (*arā kelik*) projecting

from their inner surfaces that are pierced to take lashings. Lugs are sited on the planks where ribs are intended to be fitted. There appear to be similarities between the triangular sectioned lugs on strake 5 of the *pelédang* (which support and are pegged to the lower thwarts) and the description of the lugs found on the eighth plank, the presumed sheer strake of the Butuan 5 boat (Clark *et al.* 1993: 152). A single lug is also situated at the ends of the terminal planks that make up the sheer strakes, strakes 5 and strakes 3. Lashings are passed through these lugs binding port and starboard strakes together reinforcing the junction at both stem and sternpost. *Pelédang* planks are edge-joined with wooden dowels and end to end with interlocking, stepped tongue and groove scarfs (Fig. 4). The ribs (*nulu*) are fitted over the lugs and are lashed to them with strips of *kilepa*. While most lashing was done with *kilepa*, strips of the tough skin taken from the fronds of the lontar palm, bindings of rattan were also seen. Some synthetic cordage was noted, but usually only when a makeshift repair had been effected.

Inner thwarts (*tekan*) are fitted over the lugs of the fifth strake and dowelled to them as well as being lashed to the ribs. The sheer strake (*uefi*), comprising a wide and almost full length plank and short bow and stern planks, is edge-dowelled to the fifth strake but bears no lugs on its inner surface, except at each end, and is therefore not lashed directly to the ribs. It is held down by the upper thwarts (Fig. 5). The sheer strake is not lashed to the upper thwarts as Horridge (1982: 16, fig. 9) indicates. The lashings depicted by Horridge that apparently fix thwarts to the sheer strake are, in fact, those that hold the structural supports known as *kogu* on which are attached the rattan thole bindings used with the rear oars. Horridge also unfortunately, and somewhat ambiguously, intimates in his caption to this figure that it represents a stern to stern view of the craft. The view is, however, from the bow looking aft, the lower thwarts always being situated in front of associated ribs and main thwarts.

Horridge (1982: 12) states that lashed-lug boats cannot be caulked. This is contrary to Barnes (1985: 357) who clearly states that

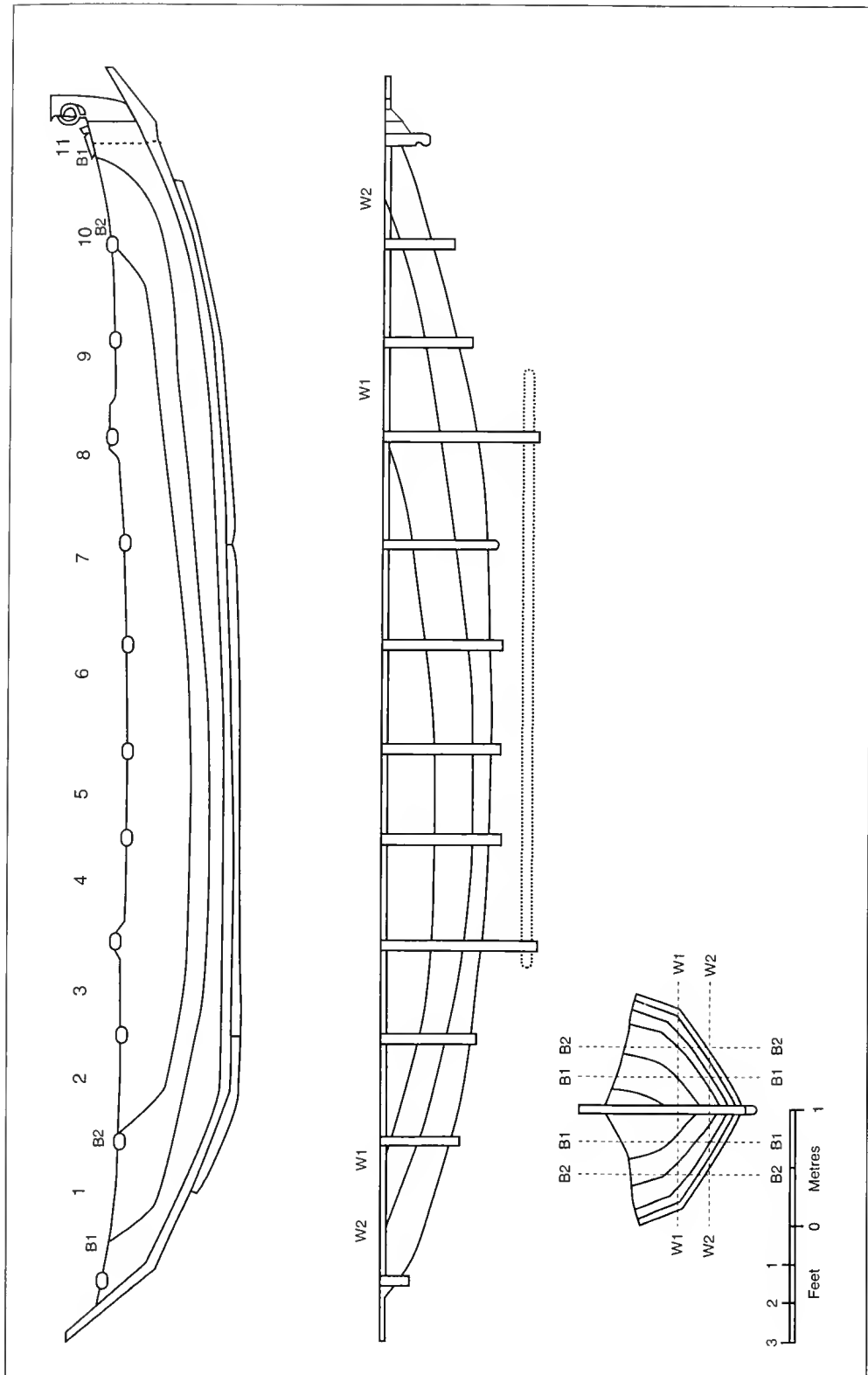


Fig. 3. Line drawing of the Lamalera *pelédang*. The rope vice (*sinabi*) reinforcing the strake/stempost union is indicated below station 11.

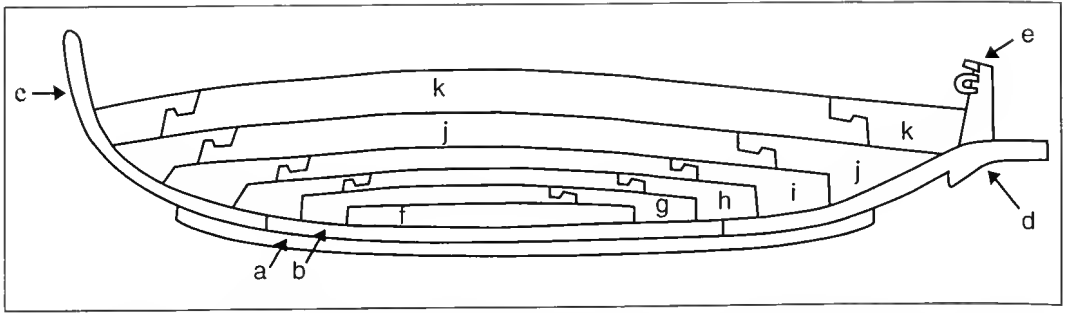


Fig. 4. Schematic representation of *pelédang* planking taken from a model of the *Téna Puka* made by Ignatius Bladan. **a.** false keel (*iyé mayi*); **b.** keel (*iyé*); **c.** - stem (*menula*); **d.** stern (*kolé*); **e.** sternpost (*madi*); **f.** strake 1 (*arā bilikang*); **g.** strake 2 (*arā kinati*); **h.** strake 3 (*arā tuka*); **i.** strake 4 (*arā nulu futu*); **j.** strake 5 (*arā bela*); **k.** sheer strake (*nefi*). Note scarfing pattern and the spur on the *kolé* which prevents the rope lashing or *sinabi* from being dislodged.

caulking, or more correctly, luting (Burningham 1989: 197), was applied during construction of the hull. Horridge (1986: 45) also states that leaking lashed-lug boats cannot be caulked. During our stay at Lamalera we regularly saw crew caulking leaking boats. Using a pointed, spatulate hardwood tool (*nilit*), a finely pounded bark fibre called *tabima* was driven into any openings visible along the plank seams.

Between the stem and stern there are placed either ten or eleven upper thwarts. The upper thwarts are notched over, and let into the sheer strake, creating a half-lapped junction. The first thwart from the stem is the *belina*. On some craft, thwart 1 rests on a short lugged plank insert (*nelu*), added to the fore end of each sheer strake. This is said to be a recent innovation. Thwart 1 and the following two thwarts support the four large bamboo poles that are lashed, two on each side of the stem, to make up the frame of the harpooner's platform (*lama*). The proximal ends of the bamboo are slotted into thwart 4. Thwarts 4 and 9 extend some 80 cm beyond the sheer strakes and also serve as outrigger booms. They are called the *gilefé fā* and the *gilefé uring* respectively. It should be noted that the outriggers (*elé*) do not, as Horridge suggests (1982: 51) function as floats, but are said to protect the hull from damage when handling whales and large manta rays. They also serve as pivoting points or fulcrum when bringing aboard large game and when assisting to right other craft that have capsized or swamped (Barnes 1980: 49; Gernot Lorber, pers. comm. 1993).

The sternmost thwart, *sepe*, serves as both a seat for the helmsman (*lama uri*) and as a fulcrum for the steering paddle (*fai uring*). The leading edge may be straight or have a semicircular concavity carved in at each end where it projects beyond the hull. These serve to hold the steering paddle in place. As well as being lashed internally, both to the hull and the sternpost (*madi*), the thwart is pierced on each side, just outboard of the hull. A strong lontar fibre rope is passed through one hole, run around the hull to sit in a notch on the sternpiece (*kolé*), up to the *sepe* and pulled tight and tied off at the other hole. Alternatively, the rope may be passed through a hole bored through the *kolé* rather than embracing it. One craft we saw used both methods. This external rope vice assists in keeping the stern planks from springing from the sternpost (*madi*) and is known as the *senabi* (Fig. 3). *Pelédang* show the vertical expansion and notch on the *kolé* when the *sinabi* is passed around it, but the feature is abandoned when the *sinabi* is passed through it. This suggests that piercing the *kolé* is a more recent innovation. This expanded lower margin of the stern piece and notch seem to be represented on depictions of Dong Son boats on bronze drums (Higham 1989: 201, fig. 4.8), suggesting that the practice of using a rope vice to keep strakes to stern post is of some antiquity. Models of *pelédang* that we purchased had the cord representing the *sinabi* going around the *kolé* and sitting immediately in front of a pronounced vertical expansion of that section (Fig. 4).

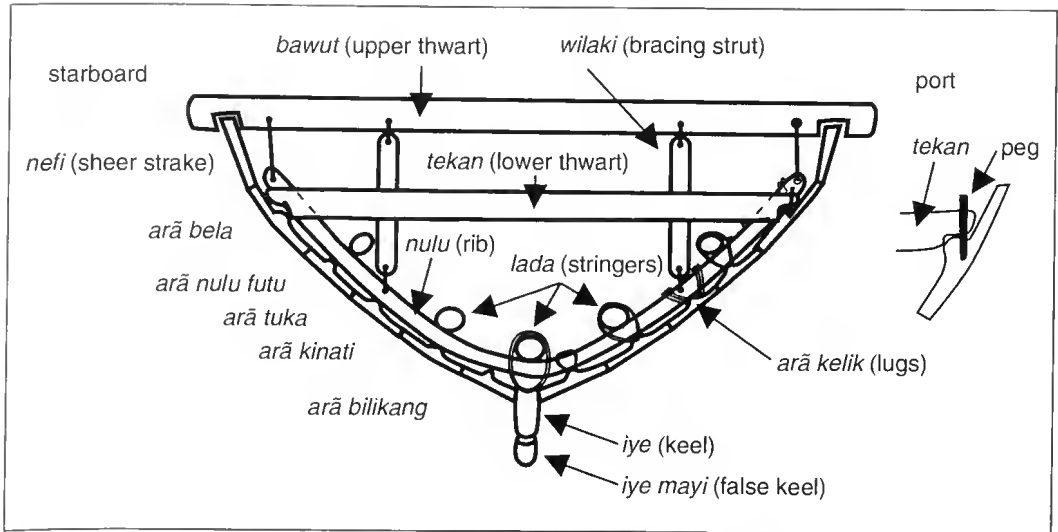


Fig. 5. Cross-section of *pelédang* showing structural features and plank nomenclature. Lashings are not shown for the starboard side. Bow to stern view at thwart 5 (*bawut puwā pukā*).

On several *pelédang* it appeared that the stern had been damaged at some stage and rather than a carefully carved and fitted *sepe* being present, a hastily cut section of tree branch had been pressed into temporary service ensuring that the *sinabi* remained effective. Horridge (1982: 16, fig. 9) illustrates such a temporary *sepe*, situated immediately in front of the projecting sternpost, in his illustration of the details of the lower hull construction of a *pelédang*. It is possible that the projection on the under side of the keel-plank of the 12th century Butuan Two boat, referred to by Clark *et al.* (1993: 158, fig. 14), indicates that a *sinabi*-type lashing was a structural feature used in the construction of ancient lashed-lugged boats. On contemporary *pelédang*, the stem ends of the sheer strakes are lashed together, the lashing being passed through a single lug on each plank. This lashing is then frapped to pull the planks tightly together. A lashing then connects the stem to the forward sheer strake lashing and is also frapped. In this way the stem is fixed to the sheer strakes and the bows firmly closed.

All upper thwarts project 15–30 cm beyond the sheer strakes and along with the outriggers provide purchase points for boat handlers when moving the craft to and from the boat sheds. These thwarts are lashed down to the top of the ribs through holes drilled in both the thwarts and ribs. Upper

thwarts 4, 5, 7 and 9 are also connected to the corresponding rib and the lug on the fourth strake by wooden battens (*wilaki*) cut to length and pierced at either end for lashing. These wooden battens seem to be safety devices, as they are only loosely attached to the thwarts and ribs and would only come under load if other lashings failed (Fig. 6). They may possibly provide real structural support if the craft is under tow, as when fast to a whale.

The thwarts divide the inner hull into a series of named compartments (types of *uak*). Compartments are named for either hull features that lie within them, after specific gear that are traditionally placed within them or for the activity that occurs at that position. Thwarts, other than those already named, take their names from the compartment immediately behind them (Fig. 7). *Pelédang* may have, depending on whether there are one or two ribs set astern of the rear outrigger boom, either 10 or 11 compartments. When there are 10 compartments, No. 9 is termed the *smugur*; when the boat has 11 compartments, No. 9 is termed the *smugur bela* and 10 the *smugur kēni*. The last section (*uak lama uri tobo*) is where the helmsman is seated. According to Barnes (1980: 20; 1985: 347), boats with 11 compartments were said to be called *tēna* while those with only 10 were classed as *sapang*. As Barnes points out (1985: 347),

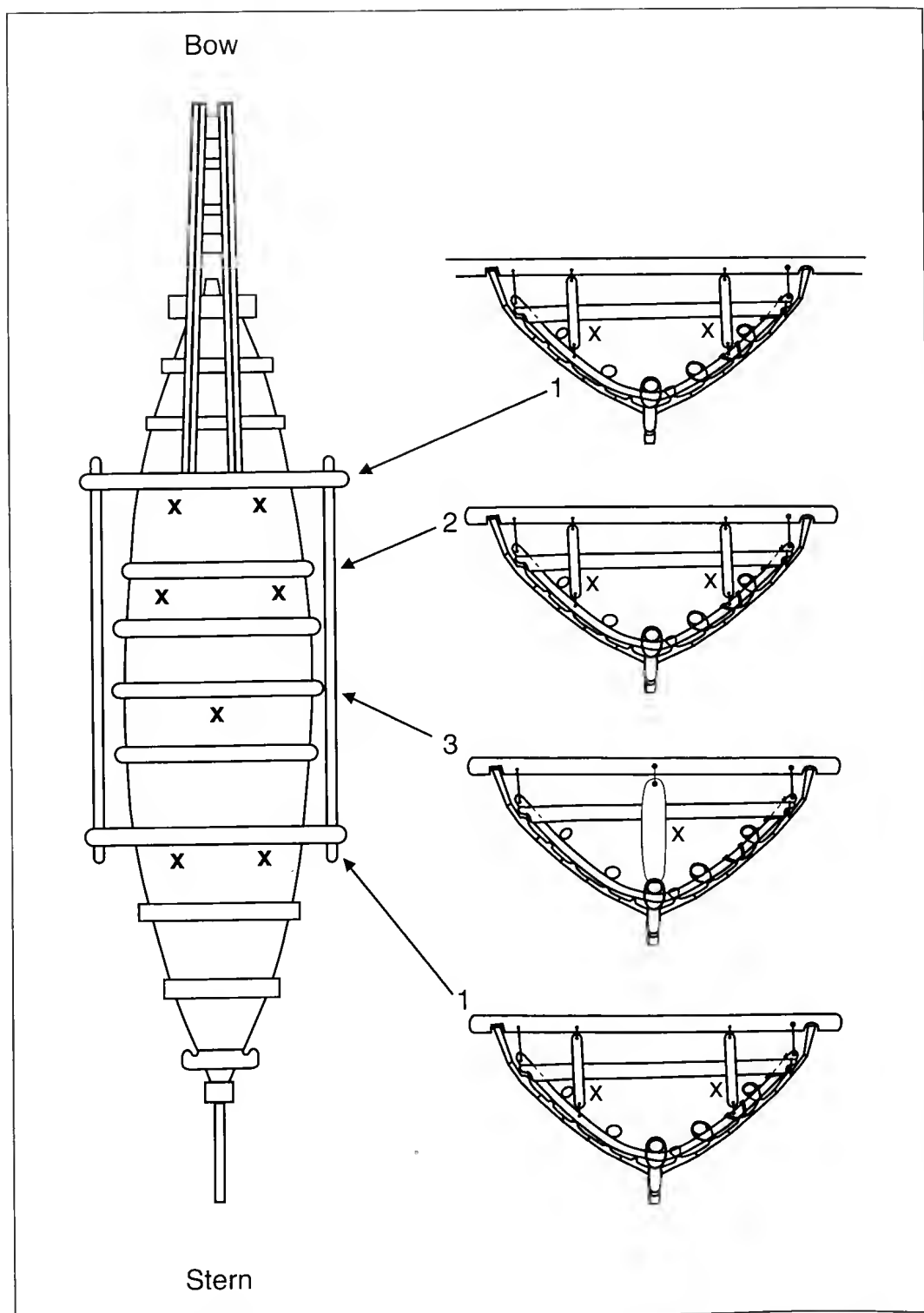


Fig. 6. Plan and stern to bow view sectional drawings of *pelédang* showing the position of the *wilaki* (x=bracing struts).

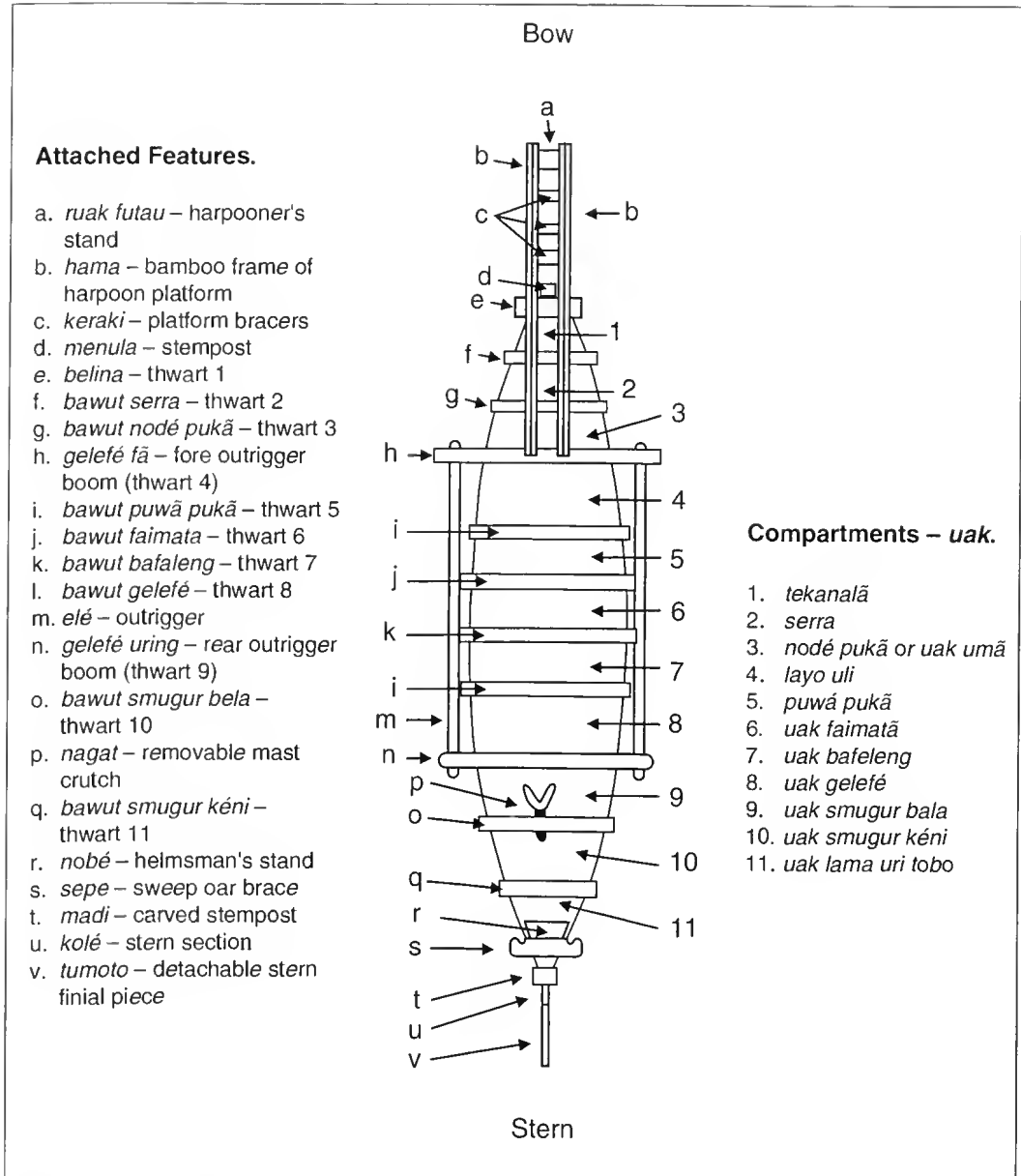


Fig. 7. Plan of *pelédang* showing major structural features, principally the thwarts (*bawut*) and open compartments (*uak*).

this explanation does not necessarily hold true today and Lamalerans suggest that any apparent irregularity in contemporary boat names relates to the designation, either *téna* or *sapang*, of the original craft bearing that name.

The keel is made up of three mortised pieces to which the stem (*menula*) and the stern extension (*kolé*) are joined at either

end. Under the keel and attached to it by wooden trunnels is a replaceable three piece false keel (*iye mayi*). Its function is to protect the structural keel during launching and beaching and the daily skidding of the boat up and down the beach, to and from the boat shed, on timber bauks laid at right angles to the path of the boat. The planks making up the six strakes are scarfed with scarfs

staggered so that no two scarf joints are in alignment, and the sheer strake provides a solid lock for the strakes below it (Fig. 4).

The hull appears to be made up of two distinct shapes—a V-sectioned lower part below a hard chine which divides it from the wide top strake (*nefi*). The five lower strakes form the double-ended underwater body (Fig. 3). The lashed-lug hulls of east Indonesia have been described as similar in some structural details and plank pattern to the traditional South Sulawesi hull (Horridge 1981: 78). Barnes (1985: 351–353), however, disputes the importance of some plank similarities and also believes that the names given to the planks indicate that the fifth strake is a recent addition. The lashed ribs are only attached to the five lower planks (Fig. 5). The stem above the fifth strake becomes more vertical where it meets the plank pieces making up the bow section of the *nefi*. The planks of the sheer and the fifth strake at bow and stern are carved to shape and not flexed to meet either stem or sternpost. *Pelédang* possess, in this mode of construction, elements of the design of a seven-part canoe, even though they are built on a keel plank with distinct stem and sternpost (Burningham 1992). Virtually all the planking below the sheer strake in the stern terminates on the keel or the keel extension (*kolé*), with only part of the fifth strake and the sheer strake terminating at the stern on the decorated vertical sternpost (*madi*). The vertical sternpost serves primarily to give attachment to the planking above the chine. The largest plank in the sheer strake (*nefi*) extends beyond all other scarf joints in the lower planking and terminates about one metre from either end of the craft. Short carved planks, extensions of the main plank, form the sharp topsides in the bow, and run the strake to the stern. The use of complex scarfed planks was noted in the Butuan Two boat and, as in the *pelédang*, these indicated a rapid change in hull shape towards each end of the vessel (Clark *et al.* 1993: 146–148). Barnes (1985: 351) notes that a softwood seventh strake is occasionally added to the hull when transporting a large cargo of game home from an extended hunting trip. We do not know how this strake was added other than

as a wash-strake, carved to fit on the sheer strake, over the fixed thwarts and lashed to them. We did see dugout canoes at villages adjacent to Lamalera which had been built up by the addition of lengths of shingled banana leaf matting, so possibly the building up of the *pelédang* was undertaken in an equally ephemeral manner. Certainly, we saw no evidence that the occasional addition of the seventh strake required any drilling or pegging of the sheer strake, and find it unlikely that the craft was dismantled to allow the additional strake to be fitted beneath the sheer.

Within the hull, a series of four stout cane stringers (*lada*) are lashed in place on top of the ribs, two on either side of the midline. A fifth is set above the keel line and either side of the central compartment (*uak fai matā*). This section is left open so that the bailers have unimpeded access to the bilge. The two outer stringers and the central one run from the second thwart (*bawut serra*) to the second last thwart (*nobé*), the latter serving as a stand for the helmsman. The two inner lateral stringers commence at the third thwart (*bawut nodé pukā*) and terminate also at the *nobé*. Below the stringers, slats of bamboo or thin flexible wands of brush are set as floating ribs (*téna kanafā*). These are set in each compartment with the exception of the first, the central and the last (Fig. 8). Two floating ribs are set per compartment if bamboo is used; three, if brushwood sticks. We do not believe these additions have a structural function in the hull, but rather serve to keep harpoon lines out of the bilge and also provide surfaces, other than the planking, on which the crew can move about the craft. We were also told that game butchered at sea was kept on the stringers and floating ribs in compartment 5 (*uak puwā pukā*).

At thwarts 3 and 7 and lashed to them on the starboard side, two wooden crutches the *nodé fā* and the *nodé uring*, are braced against the gunwale (Fig. 9). They extend about one metre beyond the gunwale and are positioned to hold the harpoon and punt poles. The furled sail is also placed on them while the mast is being lowered. The forward crutch has a lesser crutch (*nodé ipakena*) carved at the distal end. This takes the

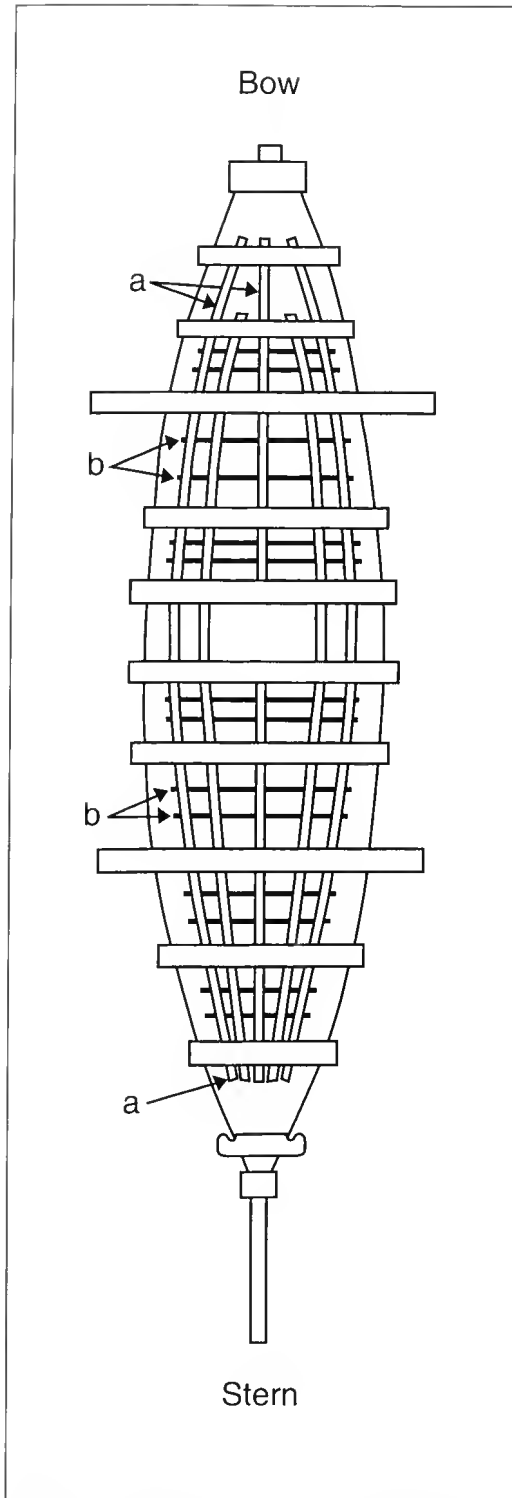


Fig. 8. *Pelédang* showing a, stringers (*lada*) and b, the floating ribs (*téna kanafe*) lashed beneath them.

proximal section of whichever harpoon is armed and ready for use. A removable crutch called the *nada* is kept in the boat at all times and is employed when the sail is being lowered on the port side. This has a notched foot which engages with the outermost stringer as it rests against the gunwale. The *nada* is also said to be used as a lever with which large game can be pulled toward the boat and dispatched.

RIG AND SAILING CHARACTERISTICS

The *pelédang* has a bipod mast (Fig. 10), consisting of two bamboo poles (*puwā*) joined by a flat, forked wooden masthead (*orā*). Each leg of the fork is fitted into the end of the bamboo poles, which are reinforced with woven rattan frappings. Further structural support is provided by lashing the masthead, through a raised and pierced lug on its rear surface, to a horizontal strut (*eda*) connecting the poles. The masthead is pierced at the apex to take the halyard. Below this aperture it is slightly constricted to take the forestay (*bela fā*) and afterstay (*bela uring*) which are made fast to it.

The lower ends of the bamboo poles are fitted with sturdy wooden stirrups (*puwā layi*), which are fitted over ends of thwart 5 (*bawut puwā pukā*) when the mast is to be raised and tied to it with a short rope called the *kabi*. The backstay remains permanently made fast to both masthead and thwart 7 (*bawut gilefē*), where a strongly curved piece of timber (*kumi*) is fixed between rib and thwart to reinforce the latter. Mast raising is accomplished by some of the crew pulling on the forestay, while others simultaneously push up the mast legs. The fixed backstay ensures that the forward rake of the mast remains constant, with the masthead positioned slightly forward of thwart 2. When in the lowered position the stirrups are slipped from the thwart, the legs are brought together and the mast lies along the midline of the craft with the upper end resting in a removable, forked cradle (*uagar*) that slots into either the rear outrigger boom (*gilefē uring*) or thwart 10 (*bawut sunugur bela*).

The sail (*laja*) is rectangular averaging 4 x 8 m (Fig. 11). It is made of a series of square

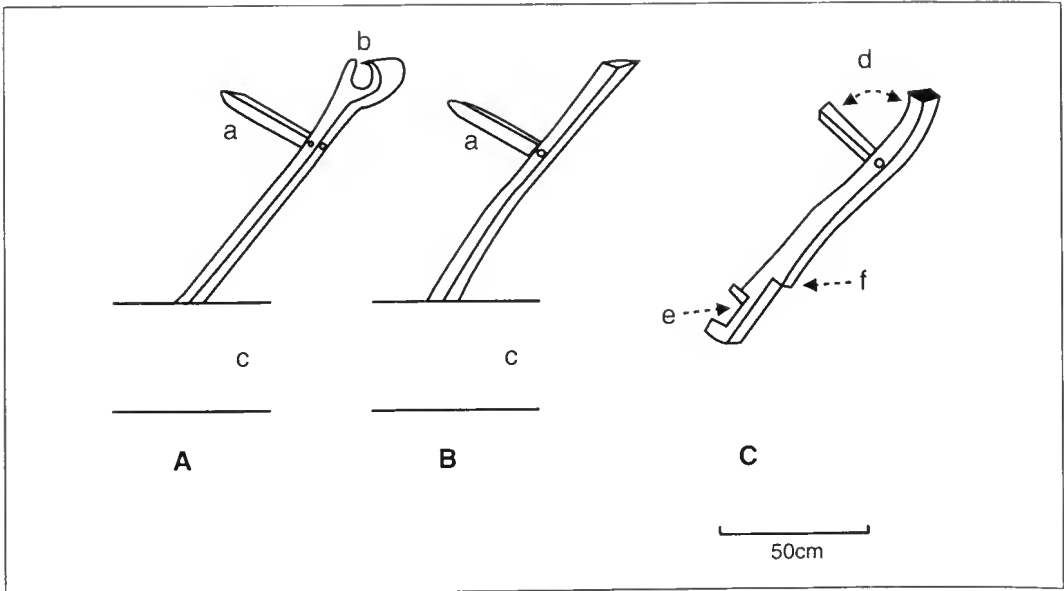


Fig. 9. A, forward harpoon pole crutch (*nodé fā*); B, aft harpoon pole crutch (*nodé uring*); C, removeable pole crutch (*nada*). a, fixed pegged arm; b, crutch to hold the active harpoon (*nodé ipakena*); c, sheer strake; d, pivoting arm; e, notch to engage outermost stringer; f, notch to engage with the gunwhale.

panels woven of prepared 10 mm wide ribbons of lontar palm frond (*kebang*) on an open cord mesh (*kelura*). Individual panels (*matā*) average 400 mm a side, and when damaged, can be individually replaced by re-weaving. The sail could be considered to be composed of strong 'rip-lock' panels that contain any tearing and prevent major damage to the sail as a whole. Weaving of the panels is done with the assistance of a wooden frame (*selaga*) which allows the sail-maker to correctly align the new work in relation to the adjacent panels. The warp is first cast as a continuous piece, spiralling from one end of the frame to the other, then using a 450 mm split-ended netting needle (*nuva*), the weft is woven in. New lengths of frond ribbon were added as required (Fig. 12). On several occasions we noted that the scraps of frond, sections of panel that had been replaced, etc, were carefully rolled up in the sail on completion of a repair, to be cast on the sea like confetti the next time the sail was raised.

The sail is set, on the longer axis, between an (upper) bamboo yard (*kelatā lolo*) and bamboo boom (*kelatē layi*). Sails may be attached to the spars with a series of individual ties of fibre cordage, but most we

saw were tied with a single running lacing (*senegat*) of synthetic cord or light rope, tied off at each end of yard or boom. The yard is suspended centrally from a single halyard (*mernami*). Barnes notes that the optimum point of balance on the yard is indicated with a mark (*kelara*), and that the halyard has to be attached at this point in order to achieve the best sailing speed (Barnes 1985: 362). At each end of the yard is made fast a long brace (*ifē lolo*). The lower spar, the boom (*kelatā layi*), is equipped with an eyed tack strop (*mernuli*) and a sheet (*ifē layi*) at each end.

When not in use the sail is kept rolled up. This is accomplished as it is being lowered, with the use of a 40 cm long wooden, truncheon-like furling pin (*manula*). This is inserted where the lower sheet and the tack strop are attached to the boom and used to rotate the latter, about which the sail is rolled. When not in use the furling pins are stowed in the bows alongside the stem. The sail is raised and unrolled simultaneously by pulling on the halyard, bringing the yard to the masthead. The halyard is then tied off close to the port mast leg so that it lies along it and out of the way. Windward brace and sheet are coiled and placed on a wooden

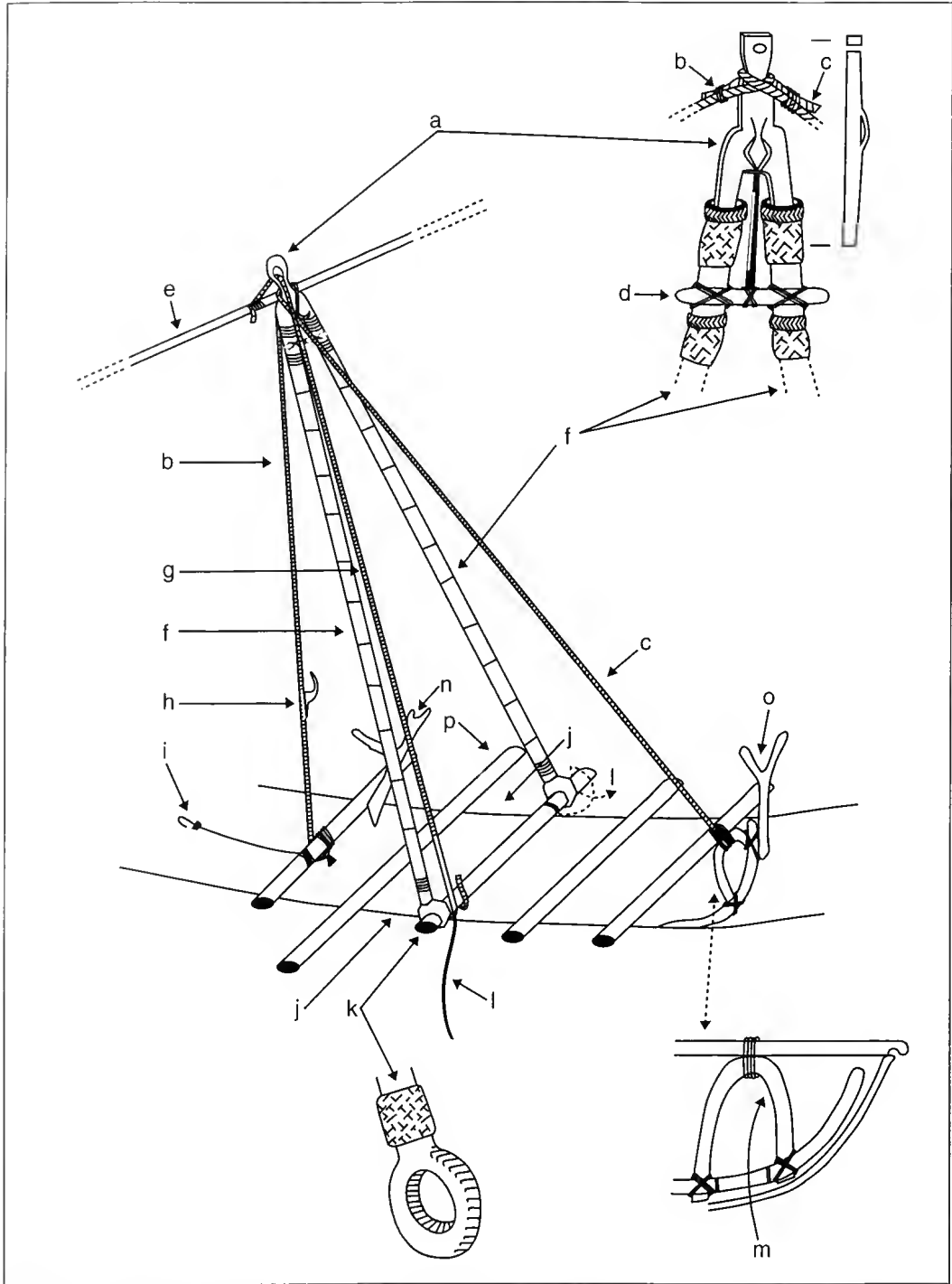


Fig.10. The *pelédang* mast and associated rigging. **a.** mast head (*orā*); **b.** fore stay (*belu fā*); **c.** backstay (*bela uring*); **d.** masthead brace (*eda*); **e.** yard (*kelatā lolo*); **f.** bamboo mast legs (*puwā*); **g.** halyard (*mernamī*); **h.** hook (*ternigi*) for stowing windward brace and sheet; **i.** clew hook (*kiuaté*); **j.** (*nubit*); **k.** mast stirrup (*puwā layi*); **l.** stirrup lashing (*kabi*); **m.** back stay tie off point reinforcing strut (*kuni*). **n.** forward harpoon and sail crutch (*uodé fā*); **o.** rear harpoon and sail crutch (*uodé uriug*).

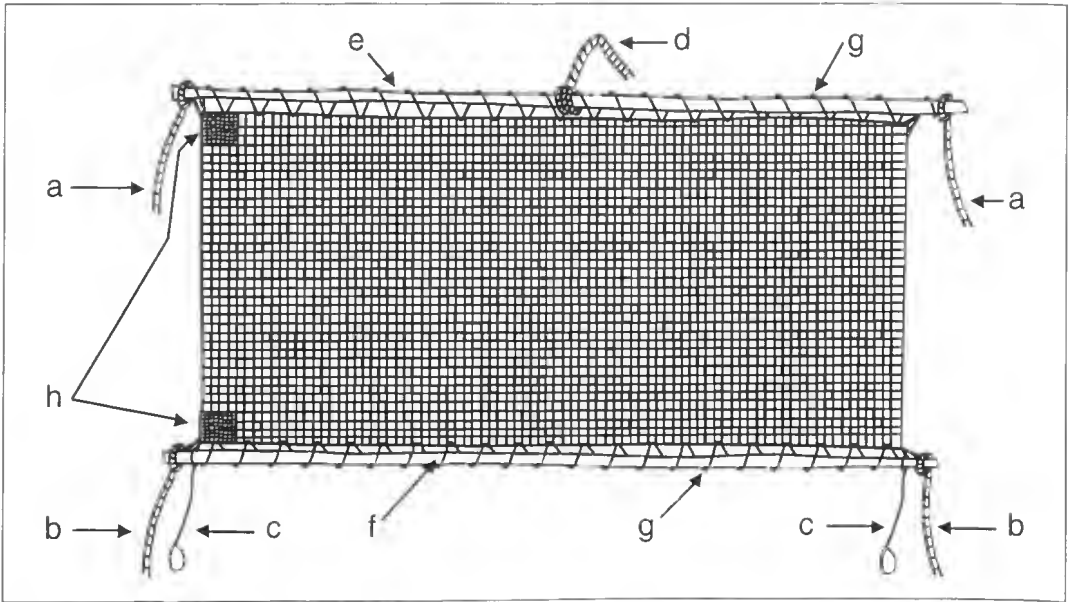


Fig. 11. The sail (*laja*). **a**, yard brace (*efe lolo*); **b**, boom sheets (*efe layi*); **c**, tack strops (*mernuli*); **d**, halyard (*mernami*); **e**, bamboo yard (*kelatā lolo*); **f**, bamboo boom (*kelatā layi*); **g**, continuous spiral binding (*senegat*) holding sail to yard and boom; **h**, woven sail panel (*matā*). The sail is made up of approximately 300 of these panels.

hook (*tenigi*) that is lashed to the forestay. The eye of the windward tack strop is then slipped over the end of the windward *nubit*. *Nubit* are backward protruding lengths of stick, lashed beneath the forward thwarts on each side of the hull and which emerge immediately aft of the forward outrigger boom (thwart 4). The leeward brace and sheet are each then taken in hand by a crew member and led aft and, when the sail is satisfactorily set, are tied off on the aft outrigger boom (thwart 9). The sheet is tied off at the leeward side and the brace at the windward side of the thwart. A hook (*kinaté*) attached to a metre long length of cord fastened to thwart 3, can be used to control the tack of the sail when sailing off the wind (Fig. 13).

Like many other sailing rigs used in the Indonesian archipelago, the *pelédang* is not tacked or turned through the wind when changing from one windward tack to another, but rather gybed or turned downwind to effect the change. Other rigs, such as the rectangular *layar tanja*, described as related to that of the *pelédang* (Horridge 1982: 53), bear only superficial similarities in the way they are operated. Like the lateen

rig or *layar leti* of Madura and Bali, when the *layar tanja* is gybed, its spars and sail are moved around the front of the mast but the leading edge and tack remain at the same end of the sail. With the *pelédang*, the sail moves across the front of the mast when gybed and that part of the sail that was previously the leach at the back of the sail now becomes the leading edge. The *layar tanja*, except on small outrigger canoes, is normally carried on a tripod mast with one leg stepped in the bow. We saw *pelédang* running down wind, the sail set with the yard square to the mast. This, along with the change of the leading edge described above, indicates that the sail is technically a true square rig. However, it is normally canted, like the canted rectangular sail or *layar tanja* of the region, which makes the sail more efficient.

The *pelédang* rig has been described as relatively weak and ineffective (Horridge 1982: 53), but we saw no evidence of this when sailing on *Holo Sapang*. With the wind at 10 to 15 knots, the *pelédang* sailed quite smartly, the rig loading the vessel sufficiently to have the lee, forward outrigger boom scooping enough water into

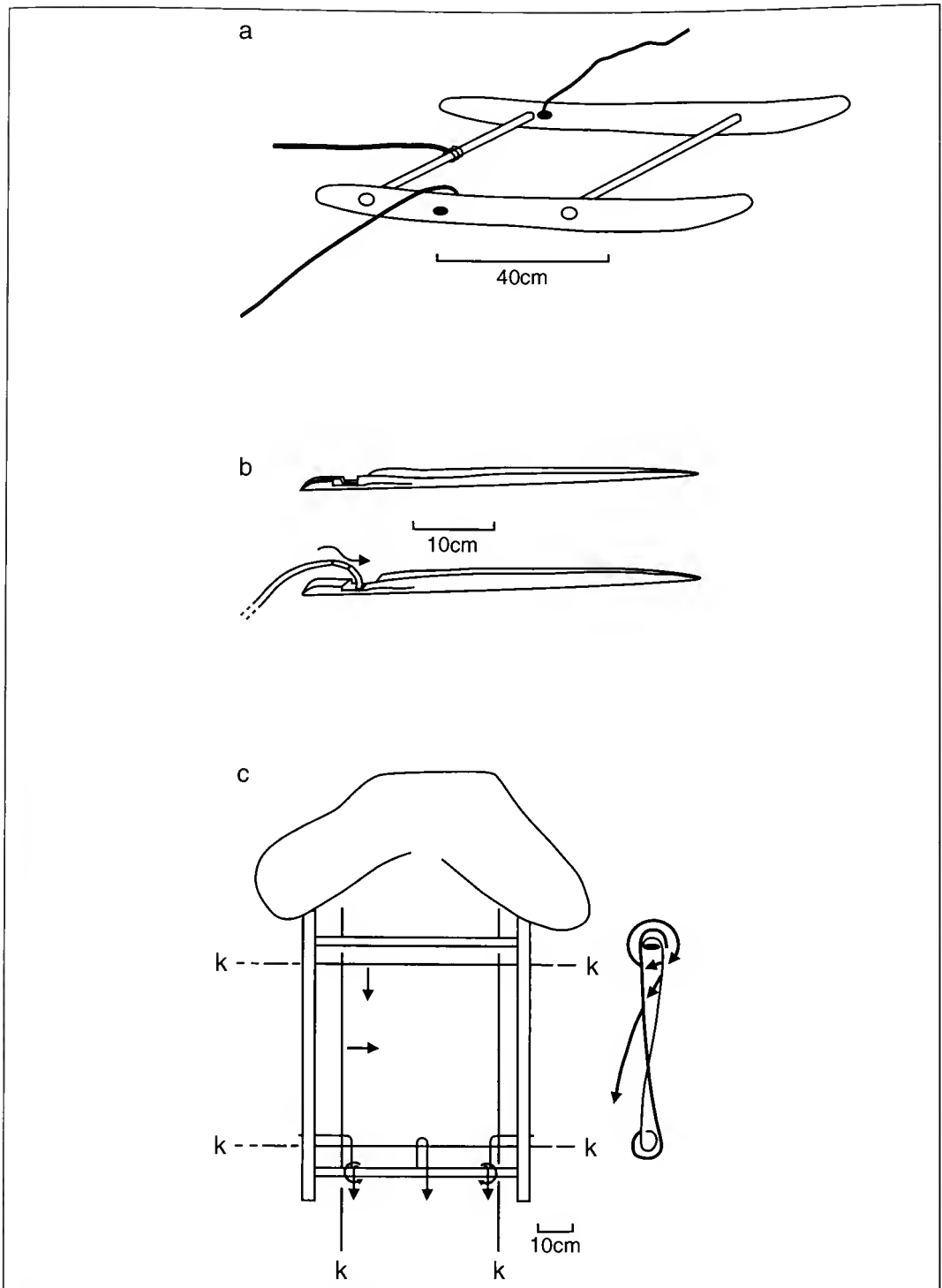


Fig. 12. a, weaving frame (*selega*). The ties are used to key the frame to the cord mesh base (*kelura*) of the sail when repairing a sail square (*matā*). b, weaving needles (*nuva*). The lower needle has a strip of prepared lontar palm frond placed in the slit ready for use. c, position of the *selega* when in use. The warp is established first and then the weft is woven in with the *nuva*, i, indicates the *kelura*.

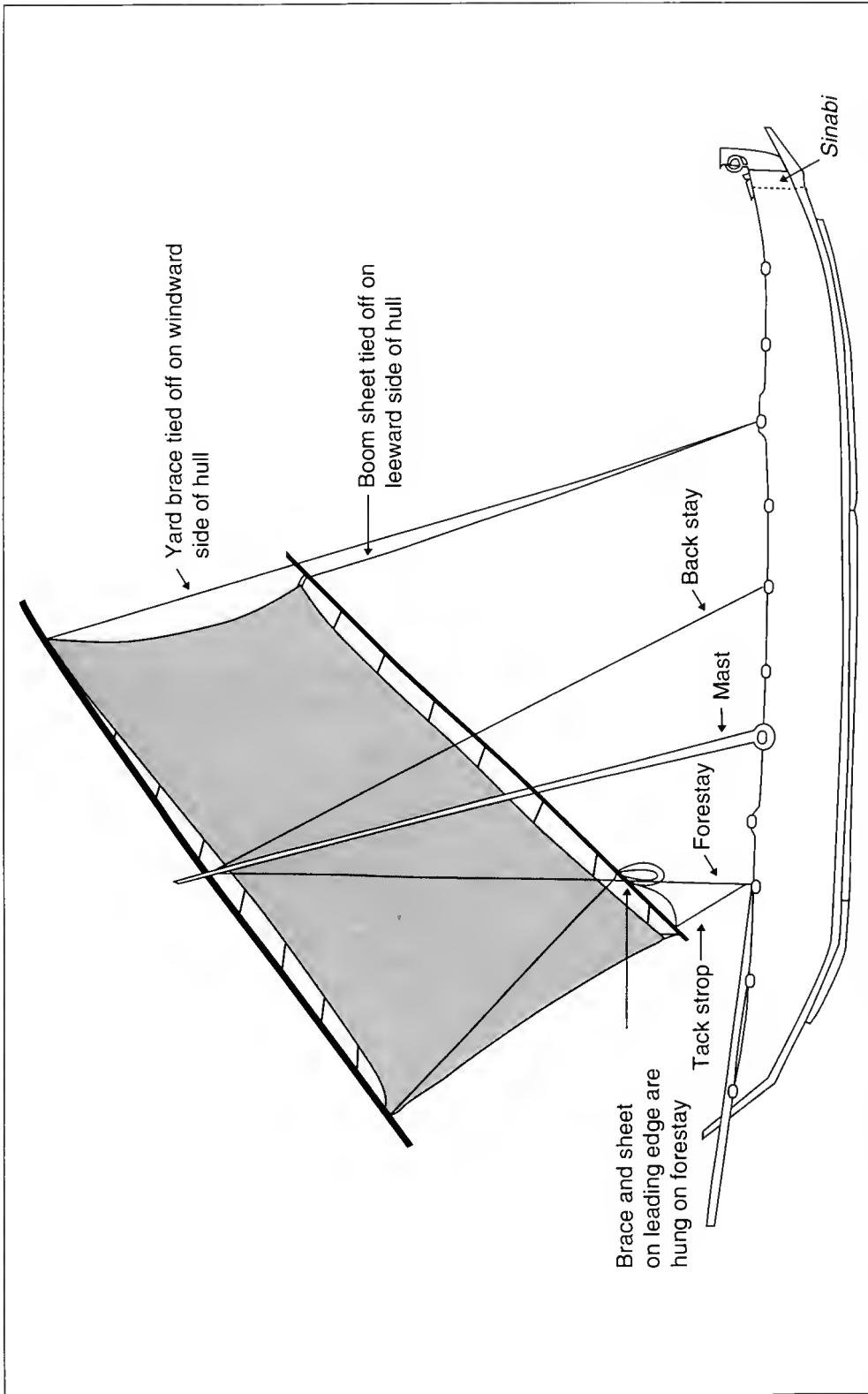


Fig. 13. *Pelédang* under sail, wind from the port beam. Sketch taken from a photograph and imposed on a hull drawn to scale. The crew, as well as structural features such as the outriggers, harpoon crutches and poles etc., have been omitted in the interests of clarity. The position of the rope vice or *sinabi*, is indicated at the stern.

the bilge to require the regular attention of the bailers. The *pelédang*, having shallow draft and a length to beam ratio of around 5:1, would be over-burdened with a larger sail plan. The ability to spill wind from the back of the sail, by easing the lower sheet whilst maintaining the course to the wind, is one of the great advantages of this rig and the *layar tanja*, as it can reduce the heel of the vessel in strong winds. As capsize is a real possibility in the hunt of large prey, such as whales, the ability to quickly lower and stow the sail and mast is a necessary feature of a whale boat. The sail and masts are always lowered prior to closing in on a whale, the final approach being effected by paddles and oars (Barnes 1974: 154).

When the *pelédang* is being launched and beached the crew propel it with paddles (*fai*) and round bladed oars (*befajā*), a pair of which are operated from both the bow and the stern. The ordinary paddles and the steering paddle (*fai uring*) are carved in the solid. The oars, however, consist of a round wooden blade lashed to a long shaft and resemble long handled table tennis bats. Where the shaft engages with the rattan thole bindings, wear marks delineate the extent of the oar loom. The forward oars are placed in loose thole bindings that are supported on forked stick rigs (*katafalé*) that are lashed and pegged between thwarts 2 and 3 on each side of the bow. At the stern, similar structures (*kogu*) serve as fulcrum for the rear oars (Fig. 14). A bamboo punt pole (*tuko téna*) is used when in shallow water to keep the craft off the rocks that stud the beach edge.

Each boat has its own shed into which it is run each evening. The boats are supported under the outrigger with forked timber props (*tenuba laki*) and along the hull with wooden blocks (*tenuba ina*). The boatsheds (*naje*) are placed at the back of the rocky beach that lies between Bawufutung Point to the northeast and Saribiya Point to the southwest. Some crew have, due to the nature of the rocky beach, access to only one area for launching and landing their craft. The state of the tide determines the launching and landing points utilised by other crews (Fig. 15). The beach itself is divided into three named zones. The

northern most section, called *Onā* services craft from sheds 1–8; the middle section, named Mobololo Beach after a turtle-shaped rock that lies awash directly off the beach (*mobo* – leatherback turtle), generally serves as the access for craft in sheds 9–18. However, if the tides are not favourable these craft are launched and landed from the third section of the beach called *Engaowā* which is also the access point for boats in the remaining sheds, 19–34.

Normally the crews assemble at their respective boat sheds at about 6 a.m. Sometimes, however, a crew cannot be made up, or the harpooner decides not to go out. In such cases the remaining crew disperse to carry out land-based tasks such as recoiling the harpoon lines, repairing sails or caulking their craft. Operational *pelédang* are always left with harpoon lines and other accessories correctly disposed about the craft, thus ensuring that it will be ready for immediate action if circumstance demands (Fig. 16). Those crews going to sea say prayers, the harpooner removes a neatly woven cover (*pelobos*) that is placed on the stempost (*menula*) whenever the craft lies in the shed and blesses the boat with holy water. Then, usually assisted by other clansmen, they skid the craft across logs or baulks of timber (*lage*) down to the sea. Timing the launch with a running sea the crew push the boat into the water and scramble aboard while others hold it steady. The crew, using the oars, paddles and punt pole clear the rocky shallows as rapidly as possible. Once clear of the beach, and if sufficient breeze is present, the mast is raised and the sail hoisted. If no breeze is present, the crew, chanting to maintain timing and morale, use paddles and oars to move the vessel out to the open sea and pick up the breeze there. The boats leave the beach as a fleet, increasing the distance between each other as they begin to hunt. Lookouts keep watch for any potential prey as well as keeping an eye on the other boats, whose movements may indicate that game has been sighted or is being taken. Generally the sail and mast remain raised when taking small game, both being lowered prior to tackling a whale. The sail and mast are also dropped before beaching.

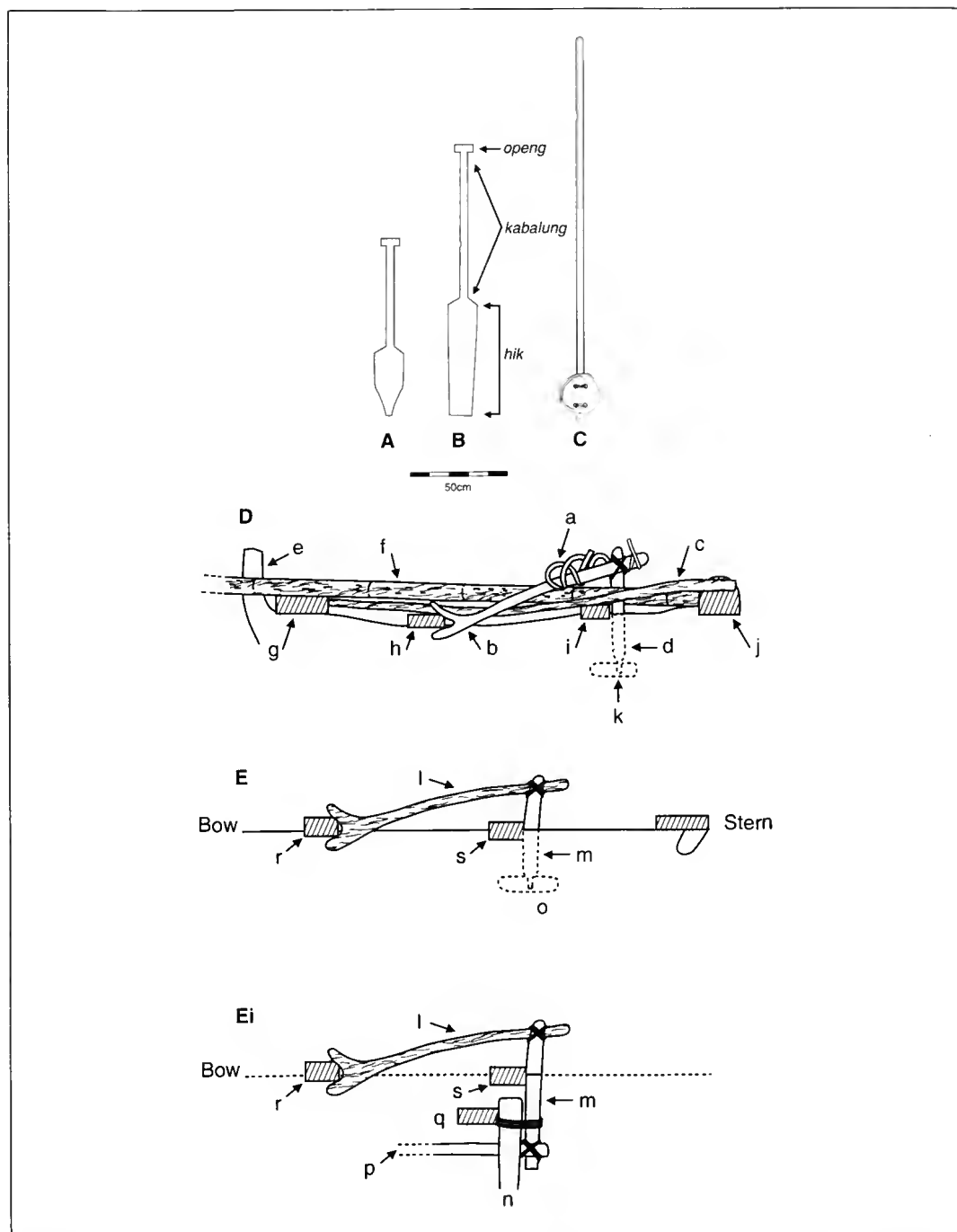


Fig. 14. A, paddle (*fai*); B, steering paddle (*fai uring*); C, oar (*befajā*); D, forward port oar station (*katafalé*); E, Rear sweep station (*kugu uring*); Ei, alternative attachment. a, loose rattan oar pivot tied to the *katafalé*; b, a forked stick lashed to and supported by the *kugu kamafer*; c, a relatively straight tree stem approximately 40 mm in diameter, fixed between thwarts 1 and 4 which serves a guide or runner for the harpoon lines, and the *katafalé nedok* (d), which is pegged into a lug on the 5th strake and also lashed to c; e, stempost; f, rear section, harpoon platform; g, thwart 1; h, thwart 2; i, thwart 3; j, thwart 4 (outrigger boom). k, lug; l, *kugu*; m, *kugu nedok*; n, rib; o, lug; p, stringer; q, inner thwart; r, thwart 10; s, thwart 11.

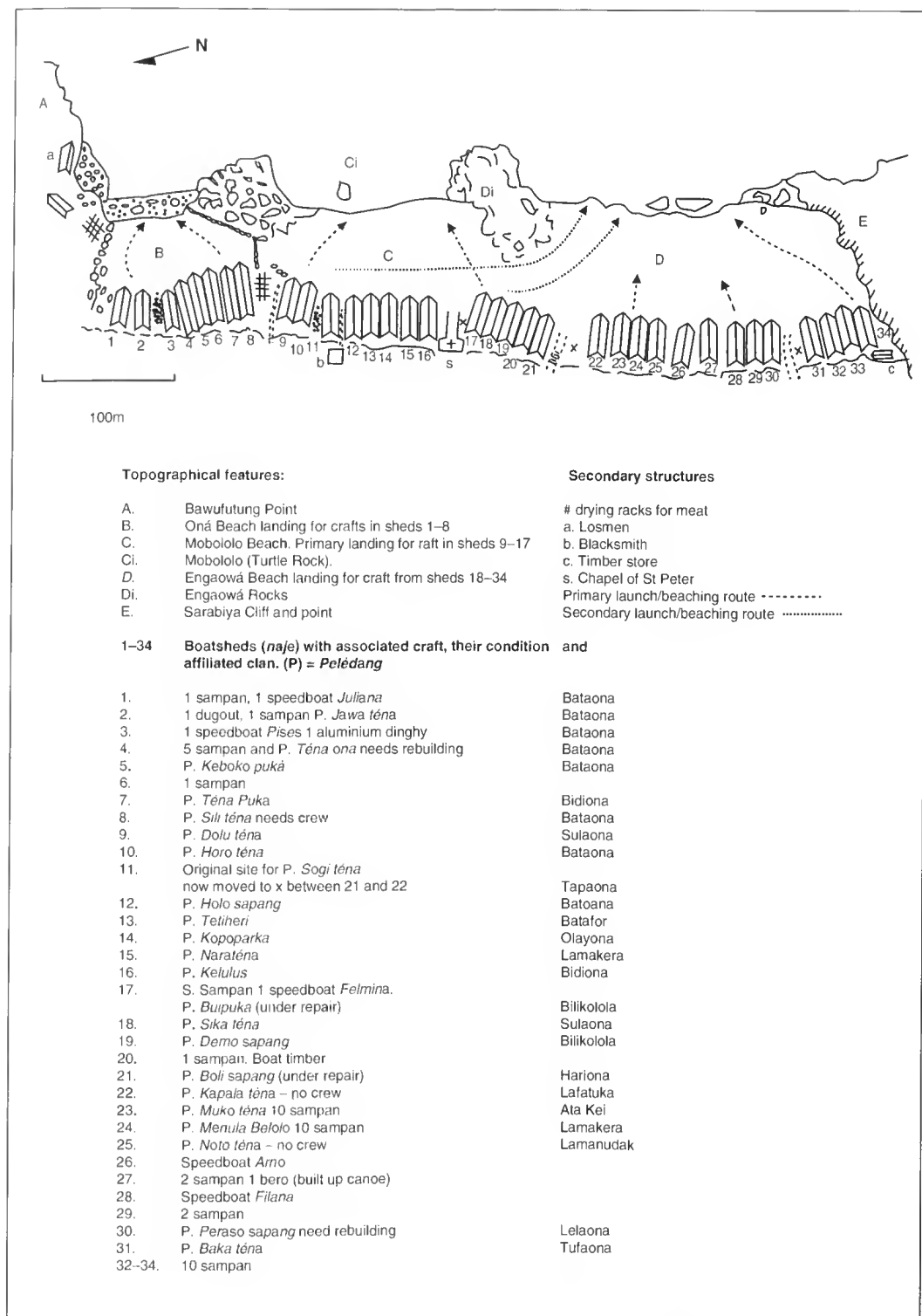


Fig. 15. Sketch map showing the disposition of boat sheds in relation to the beach at Lamalera with details of the craft etc. housed in them.

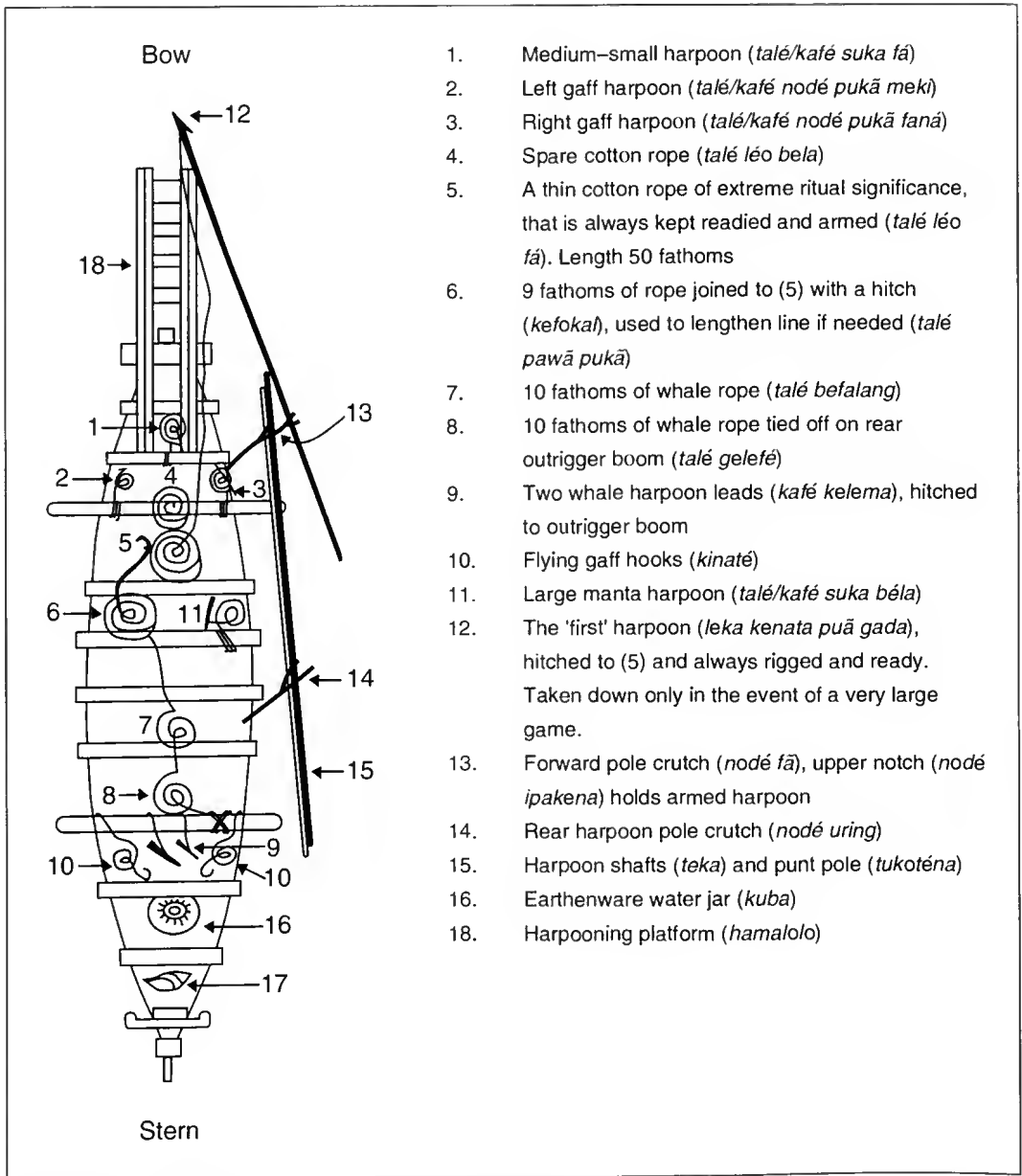


Fig. 16. Plan of *pelédang* showing the layout of harpoon lines (*talé*), harpoons (*kafé*), poles (*leka*) and sundry other gear.

Of the twenty-three *pelédang* housed on the beach at Lamalera while we were there, only sixteen were operational. For the rest, three craft were not operating for lack of a crew, two needed repairs and two others needed extensive rebuilding. According to Barnes there were twenty-five boats operating in 1969 and fifteen in the period between 1973-75. In 1979-80, of the

twenty-nine boats present, nineteen were operational (Barnes 1980: 38). Fuchs (1984: 26) recorded at least fifteen operational craft in 1984. In 1987 Masyhur (1987: 34) recorded that of twenty-seven boats present at Lamalera, only ten put to sea. Cross-checking Barnes's (1980) lists with our own information allowed us to determine that six craft were no longer extant. These were *Sinu*

Sapang, Léla Sapang, Dato Téna, Geleko Téna, Bokololo and the *Sia Apu*. These craft had been either lost at sea or on sustaining serious damage, had been completely broken down and the timbers stored or discarded. Some sheds held small canoes and one held the hull of the last traditionally built, lash-lugged canoe (*bero*) to be found in the village. Sketches and notes were made of this craft and measurements taken. Four motorised speed boats, used primarily to take smaller game and occasionally to ferry tourists to Lewolaba and Lantuka, were also housed in the sheds.

Between the boat sheds, wood or bamboo racks (*pilaya*) hold sliced whale and ray meat to dry in the sun and the wind. Some racks hold strips of blubber (*forā*) that leak oil (*lalā*) that is collected either in long wooden troughs (*noraj*) suspended beneath the blubber, or funnelled via tin guttering into bamboo containers (*nafi lalā*). Whale oil lamps (*pelita*) were still in use in some residences during our visit. Pressure lamps and electricity (provided by the church, and only available between 6 and 9 p.m.) were other sources of illumination available to the villagers. Large woven fish traps and stocks of boat timbers are also stored adjacent to the sheds or in lofts above the boats.

Timbers derived from damaged or broken up craft may be incorporated when constructing a new *pelédang*. The new craft will bear the name of the boat it replaces in the fleet. The same names can be traced back through time. According to Barnes (1980: 20), two craft bore names that are said to have belonged to boats that brought the ancestors of the Lamalerans to Lomblen.

Whether the hunting economy of the Lamalerans will further decline is a moot point. The ill-fated attempt to introduce modern technology into the village (Barnes 1980, 1984) could easily have had disastrous effects on the village. Fortunately the village and the villagers appear to have survived the experience. While there has been a decline in the numbers of people (and consequently vessels) involved in hunting, we believe that further decline may not occur. The cash input provided by the growing numbers of tourists who visit the region and who often wish to sail with the fleet, may well be an

inducement to younger members of the village to stay there rather than seek employment elsewhere.

Perhaps in this way Lamalera will be able to maintain continuity with its past. The *pelédang* will continue to be built and rebuilt and the soul, or spiritual essence, maintained in harmony with both the members of the clan who work in it and the game, especially whales, it hunts.

ACKNOWLEDGMENTS

Our warmest thanks must go to Josephus and Imelda Bataona who were our most gracious hosts while at Lamalera. We must also acknowledge the generous patience shown by Petrus Koli and the crew of the *Holo Sapang* in enduring our tedious curiosity. To our referees Mr Nick Burningham and Professor Campbell Macknight goes our sincere appreciation for their most valuable comments and direction. Finally we thank Nadene Jones for producing such excellent figures from the scrawls extracted from our diaries.

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Accepted 2 March, 1997

APPENDIX - THE DIVISION OF GAME IN LAMALERA.

The following sketches (Figs 17–21) of butchering patterns utilised when dividing major game species were made on the beach at Lamalera. We did not witness the butchering of a sperm whale and the information is derived from discussions with Josephus Bataona. All manta ray we saw were divided into the major cuts at sea, these portions were then further reduced on the beach. We failed to record the recipients of the portions of pilot whale we saw being butchered and all ocean sunfishes were filleted at sea.

The meat is distributed in set ways that differ from species to species. The initial distribution of large game usually involves the following structures or individuals.

- 1) Corporation – the associated patrilineal descent group that makes up a clan and which owns and is responsible for one or more boats depending on the size of the clan.
- 2) Corporation or clan ceremonial/meeting house (*tango ikan belifu / tango béla*)
- 3) Lord of the boat (*téna alap*). Head of the corporation.
- 4) Lords of the Land (*tana alap*). These are the senior men of the two inland villages from which the original settlers of Lamalera received permission to occupy the area (Barnes 1989: 3, 113–122). Corporations and their boats associated with boat sheds 1–16 (Fig 13) owe allegiance to one *téna alap*, those associated with sheds 17–34 with the other.
- 5) Harpooner (*lamā fā*)
- 6) Assistant harpooner (*breun alap*).
- 7) Crew (*mattros / meng*)
- 8) Helmsman (*fai uring*)
- 9) Ropemaker (*lunka talé*).
- 10) Blacksmith (*ota mola teka kafé*)
- 11) Carpenters, boat builders, sailmakers (*ata molan*)
- 12) Boat handlers

The level of distribution becomes more complex as primary recipients then divide their share according to individual patterns of obligations and duties. For further details regarding the distribution of game the reader is directed to Barnes (1980: 27–37).

Meat that is not required for immediate consumption is reduced to thin fillets that are dried on racks in the sun and wind. When dry, the meat is stored for future use. Bones are sectioned and dried and ultimately used to make broth. Few bone implements were seen; swifts (*memwa*) used to wind homespun cotton were often stood on a whale vertebra base and the drop spindles (*kiduka*) by which cotton was spun were weighted with shark vertebra whorls. Barnes (1989: plate 18) illustrates a weaving sword made from whalebone, possibly a strip taken from the long, straight and dense bone of a sperm whale mandible.

Dried meat is traded each week at local markets in other centres adjacent to Lamalera. Hembree

(1980: 40) lists forty Lomblen markets or villages at which whale meat (and presumably other marine products) from Lamalera is exchanged. Meat is exchanged in return for cassava, maize and other vegetables, fruit, cotton and tobacco—crops grown by the hill people of Lomblen. A *prahu*, selling rice from South Sulawesi, arrived at Wulandoni on the Saturday we attended market there. The next day it dropped anchor at Lamalera and attempted to sell rice for cash at Lamalera. Noting that the price of rice had escalated sharply from that quoted at Wulandoni the previous day, no Lamalerans were interested in buying from the traders.

As Barnes (1974: 139) noted ‘No other village on the island (and few in the area) is so divorced from agriculture or depends so much on fishing...’. With no arable land it is from the sea they reap their harvest, a harvest that allows them to access terrestrial crops and obtain the other necessities of life.

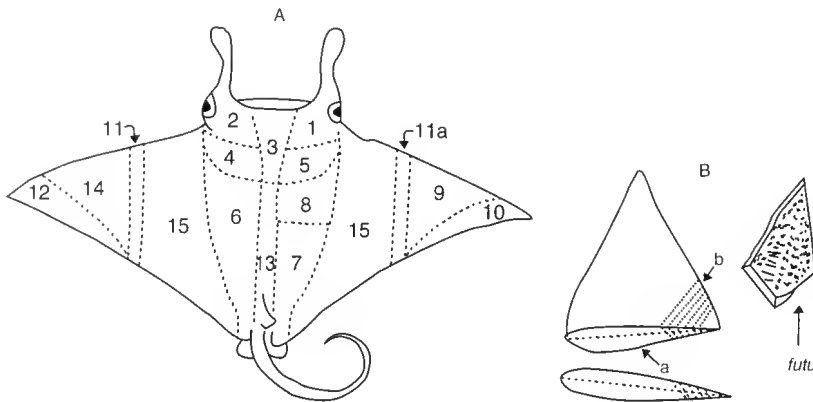


Fig. 17. A, division of manta rays (*pari*). Three types of manta ray appear to be recognised. Two of the names may reflect different stages in the growth and maturation of the giant manta ray (*Manta birostris*), or represent another species altogether. The smaller are known as *bon* and the larger are called *belalang*. The smallest ray taken is the *moku* or devil ray (*Mobula ereegoodooenkee*). The schema presented is applicable to the two larger rays. If the manta has been feeding and there is fresh krill (*kujā*) in the stomach it is saved and used as a sambal or food flavouring. B, wing being cut into kite-shaped steaks or *futu* (harpoon tip). 1, *teruk vana* (right) - the upper portion goes to the boat bailers who sit in the central section of the craft. Lower jaw and lower section of gills goes to the person who first sighted the ray. 2, *teruk meki* (left) - as for portion 1. 3, *tobanga* - gills and brain to the hailer. 4 and 5, *kotolong meki* and *kotolong vana* respectively) - divided among the crew. Gills go to the person who sighted the ray. 6 and 7, *uklolo meki* and *uklolo vana* goes to the corporation. 8, *layi maké* and 9, *topu vana* goes to the harpooner. 10, *mada vana* goes to the harpooner. 11, *bekat meki* goes to the crew. 11a, *bekat vana* goes to the harpooner. 12, *mada meki* - placed into the boat shed. 13, *iku* (tail and spine) to the crew. 14, *topu meki* - this piece is given to a different member of the crew each time a ray is butchered. 15, the rest of the wing or *laja* is cut into steaks which are divided among the crew.

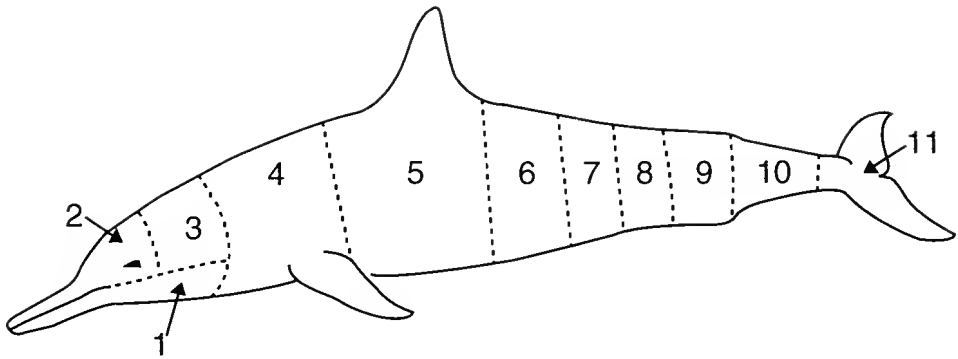


Fig. 18. Division of spinner dolphin (*temu kira*). 1, *mima* (the lower jaw) goes to the corporation. 2, *noivā* (upper jaw and head) goes to the person who first sighted the animal. 3, *tutam tikam* goes to the harpooner. 4, *kelik* is divided longitudinally. One half goes to the harpooner, the other to the ceremonial house. The heart and lungs within the body cavity goes to the blacksmith who forged the harpoons. 5, *matross* is divided amongst the crew. 6, *kofokeseba* is divided among members of the corporation owning the craft. 7, *ata molan* is divided among the craftsmen (boatbuilders, carpenters, sailmakers etc.) who keep the boat in good repair. 8, *tenarap* goes to the corporation. 9, *killā* goes to the corporation. 10, *fadar* is divided among the people who help launch and land the boats. 11, *iku laja*. Half is divided between the crew, the other half goes to the boat. That is, the crew utilises it to reinforce their own solidarity as a unit. It may be sold for tuak and the crew hold a party.

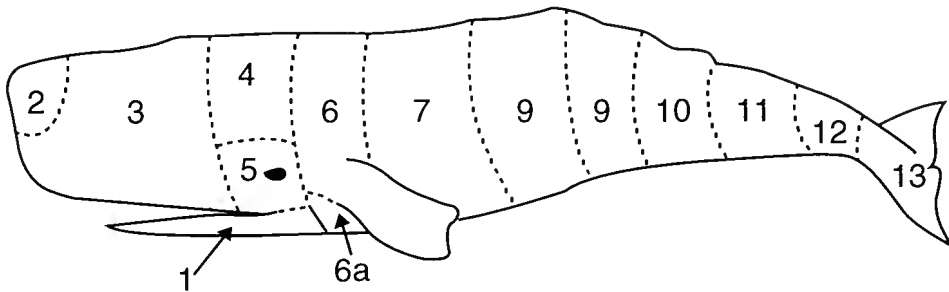


Fig. 19. Division of sperm whales (*kotan kelema*). 1, *mima* goes to the corporation; the teeth may be sold. 2, is sent to the lord of the land. 3, *lefotana* is divided among the crew. 4, *noivā* goes to the harpooner. 5, is sent to the lord of the land. 6, *belada* is longitudinally developed. The left side goes to the corporation ceremonial centre, the harpooner takes the right side. The internal organs contained in this section go to the blacksmith who forged the harpoons and to the harpooner. 7, *main* is divided between the crew. 8, *kofokeseba* is divided between the crew. 9, *lobo kotelo* is divided among the artisans who keep the craft maintained. 10, *tenarap* goes to the corporation. 11, *killā* goes to the corporation. 12, *fadar* is divided among the helpers on the beach. 13, *iku laja* is divided and the crew share one half. The other half belongs to the boat crew as a unit who may sell it to have a celebration.

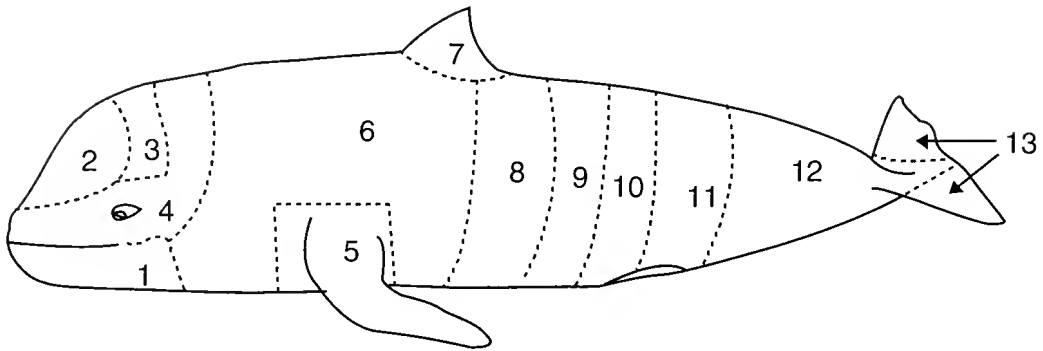


Fig 20. Divisions of a pilot whale (*temu bela*). Recipients not recorded. **1**, *mima* (lower jaw) and *evel* (tongue). **2**, *koreng* (forehead), which is further divided longitudinally. **3**, *noying*, the remaining section of the melon including the blowhole. **4**, *kota kepela* (skull). **5**, *kellik*, in two portions, each about a pectoral fin to the ventral midline. **6**, *tana kanafā* (trunk). **7**, *iting* (dorsal fin). **8**, *pefa keseba*. **9**, *laba ketelo*. **10**, *tenarap*. This section terminates about half way down the genital slit. **11**, *killā*. **12**, *fadar*. **13**, *iku* (tail flukes).

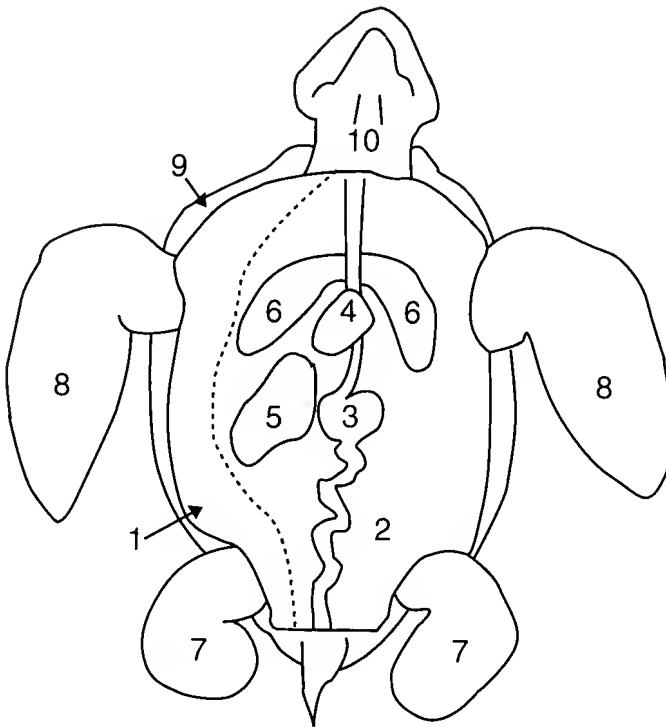


Fig. 21. Division of leatherback turtles (*mobo*). **1**, *nuli* (plastron). Goes to the corporation to assist in meeting costs of maintaining the craft. **2**, *korok* (intestines). Divided among the crew. **3**, *taying* (stomach). Goes to the boat crew as a unit. **4**, *puo* (heart). Goes to the boat crew as a unit. **5**, *ona* (liver). Divided into halves. The crew divide one half between themselves, the other they dispose of for the benefit of the crew as a unit. **6**, *furā* (lungs). The crew divide one lung among themselves, the other they dispose of for the benefit of the crew as a unit. **7**, *kepalik uring* (rear flippers). These go to the corporation. **8**, *kepalik fā* (front flippers). One goes to the harpooner, the other to the corporation. **9**, *gordung* (upper shell or carapace) is disposed of to the benefit of the crew as a unit. **10**, *kotā* or *noi alap* (head) goes to the person who sighted the turtle first.

PRISTINA PROBOSCIDEA AND *PRISTINELLA OSBORNI* (OLIGOCHAETA, NAIDIDAE) FROM A FRESHWATER CREEK NEAR DARWIN, NORTHERN TERRITORY, AUSTRALIA, WITH DESCRIPTIONS OF THE GENITAL ORGANS OF BOTH SPECIES

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ABSTRACT

Naidid oligochaetes from a freshwater creek feeding into West Arm, Darwin Harbour, were collected in July 1993. The majority of the worms were in different stages of sexual maturity. They represent two species, *Pristina proboscidea* Beddard, 1896, and *Pristinella osborni* (Walton, 1906). In this paper, full descriptions of both somatic and genital features of these taxa are given. Taxonomic and phylogenetic aspects are discussed.

KEYWORDS: Naididae, Oligochaeta, *Pristina*, *Pristinella*, taxonomy, zoogeography

INTRODUCTION

The Naididae, with a total of about 175 species in about 25 genera worldwide, comprise a considerable part of the freshwater oligochaete fauna of all continents except Antarctica. Several genera and species of this family are more or less cosmopolitan, occurring in virtually all kinds of freshwater habitats. There is a surprising coincidence in the number of species found on the different continents: 54 species are known from Europe, 81 from Asia, 51 from Africa, 55 from North America, and 52 from South America (Brinkhurst and Jamieson 1971; Brinkhurst 1986; Harman *et al.* 1988; Grimm 1987; Semernoy and Timm 1994). The high score of Asian species mainly depends on the fact that Lake Baikal, with its many endemic taxa, has been extensively studied by Russian workers (Semernoy and Timm 1994). Some of these species are, however, briefly described. A recent compilation of

records of microdrile Oligochaeta from inland waters of Australia (Pinder and Brinkhurst 1994) includes 31 species of Naididae, but it can be expected that this number will increase when additional habitats have been investigated.

The wide distribution of the Naididae is largely due to their opportunistic strategy of asexual reproduction as the normal ease. For many naidid species, reproductive organs have never been described, which is unsatisfactory, as the classification and phylogenetic assessment of oligochaetes are largely based on the position and morphology of these structures.

While participating in the Sixth International Marine Biological Workshop on the Marine Flora and Fauna of Darwin Harbour, at Mandorah, near Darwin (Northern Territory, Australia) in July 1993, the first author collected a few naidid oligochaetes from a freshwater creek feeding into West Arm, Darwin Harbour. The majority of these worms were in different

stages of sexual maturity. The material represents two species, *Pristina proboscidea* Beddard, 1896, and *Pristinella osborni* (Walton, 1906), both widespread in the tropics, but never before reported as sexually mature. In this paper, full descriptions of both somatic and genital features of the two taxa are given, and some taxonomic and phylogenetic aspects of these findings are discussed.

Other material of (largely marine) oligochaetes collected during the Darwin Harbour workshop has been published separately (Coates and Stacey 1997; Erséus 1997; Healy and Coates 1997).

METHODS

The sand from the creek was repeatedly stirred with habitat water and the organic suspensions decanted into a fine-mesh sieve (250 µm). Live worms were sorted under a dissecting microscope and fixed in Bouin's fluid. After about one day, they were transferred into 70% ethanol. All specimens were stained in alcoholic paracarmine and mounted whole in Canada balsam. Material of both species is deposited in the Museum and Art Gallery of the Northern Territory (NTM). Some specimens of *Pristina proboscidea* are also lodged in the Swedish Museum of Natural History (SMNH), Stockholm.

In the descriptions, segment numbers are denoted by Roman numerals.

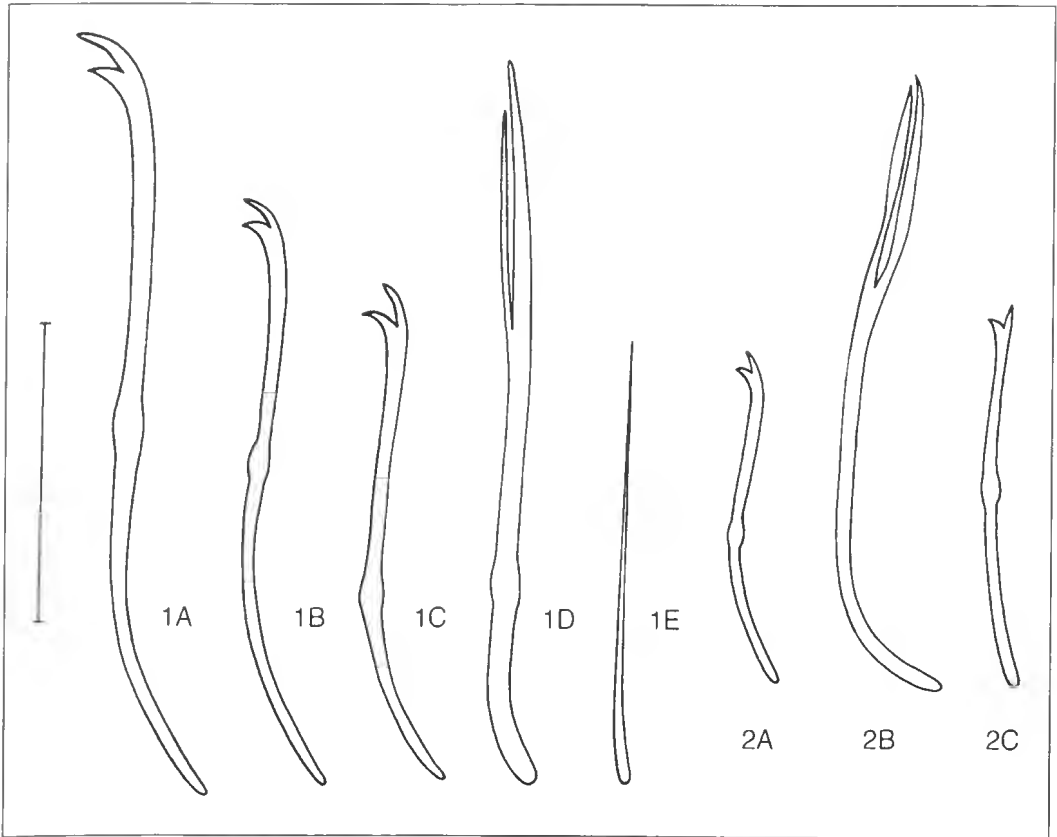
Pristina proboscidea Beddard, 1896 (Figs 1, 3)

Material studied. NTM Wo 0121–0127, 7 whole-mounted specimens, and SMNH Main coll. 1615–1618, 4 whole-mounted specimens; all from small freshwater creek feeding into Stephens Creek, West Arm, Darwin Harbour, Northern Territory, Australia, 12°38'S, 131°43'E, sand with roots and debris along a short stretch of pools and rapids; coll. C. Erséus, 15 July 1993 (CE station no. 35).

Description. Ten specimens in various stages of sexual maturity, and one immature chain with two zooids. Two complete

specimens (one mature, plus the immature worm) both 3.5 mm long (contracted), consisting of a total of 46 and 35 segments, respectively. Anterior zooid of immature worm with 21 segments. Prostomium with proboscis (Fig. 3A). Clitellum extending over VIII–IX, when developed. Dorsal setae: hairs one to four per bundle, serrate, about 200 µm long, none especially elongated; needles one to four per bundle, straight, single-pointed with fine tips, and without nodulus, 42–49 µm long. Ventral setae three to seven per bundle in II–III, five to seven per bundle in IV, four to eight per bundle in V, up to seven per bundle in VI of asexual specimens, up to nine per bundle in following segments, decreasing to mostly five per bundle further towards the posterior. All setae bifid, with distal prong slightly longer than proximal (Fig. 1A–C). Ventral setae of II–V 54–60 µm long, posterior ventral setae 48–58 µm long. One specimen with ventral setae in II and III longer (63–78 µm) and thicker than the rest. In VI of specimens in an advanced stage of sexual maturity, ventral setae (genital setae; Figs 1D: 3B: gs) about 70 µm long, bifid with prolonged straight, parallel, teeth comprising one third of setal length, and with nodulus at one third from proximal end (Fig. 1D). One specimen of full sexual maturity with one slightly modified bifid seta representing each ventral bundle in VIII (Fig. 1C). In yet another mature specimen (depicted in Fig. 3B), ventral setae of VIII lacking. Male and spermathecal pores paired, in line with ventral setae; male pores anterior to middle of VIII, spermathecal pores immediately posterior to furrow between VI and VII.

Pharyngeal glands in III–V. Coelomocytes few, spherical, each with a distinct nucleus surrounded by weakly granulated cytoplasm. Transition from oesophagus to stomach inconspicuous, somewhere behind VII (marked by presence of gut content). Male genitalia (Fig. 3B) paired. Sperm funnel indistinct, position and shape (indicated in Fig. 3B) deduced from adhering spermatozoa and position of vas deferens. Vas deferens and atrium a continuous tubular male duct, at least about 375 µm long. Proximal end of male duct (Fig. 3B: vd), a short, naked part of vas



Figs 1–2. *Pristina proboscidea*: **1A**, elongate ventral seta in segment II; **1B**, normal posterior ventral seta; **1C**, single ventral seta in VIII; **1D**, genital seta in VI; **1E**, dorsal needle seta. *Pristinella osborni*: **2A**, posterior ventral seta; **2B**, genital seta in VI; **2C**, dorsal needle seta. Scale: 30 μ m.

deferens, up to about 15 μ m wide. Middle part of male duct, i.e. remaining part of vas deferens, embedded in continuous mass of tightly packed, heavily granulated, prostate cells (pr); this part of duct ciliated, somewhat coiled, but very difficult to follow throughout its length. Distal part of male duct (a) a naked atrium, about 170 μ m long, 12–18 μ m wide, terminally opening to the exterior through inconspicuous pore; atrium appears non-ciliated. No part of male duct with notable muscular layer. Spermathecae (Fig. 3B: s) small and club-shaped, each with duct, about 35 μ m long, and about 28 μ m wide, and an oval ampulla, about 60 μ m long, and about 45 μ m wide. In one specimen (Fig. 3B), spermathecal ampullae containing loose masses of stained material reminiscent of sperm, but these 'spermatozoa' much shorter than those adhering to sperm funnel.

Remarks. The first description of *Pristina proboscidea* was given by Beddard (1896). It was based on two South American sexually immature specimens and is rather incomplete. Sperber (1948) redescribed the species as completely as it was then possible. The specimens of the present study fit Sperber's description with the exception of slight differences in the number of ventral setae in the anterior segments, which, however, lie within the variability usual for naidids.

Pristina proboscidea has been considered to be closely related to the highly variable *P. longiseta* Ehrenberg, 1828 (c.g., Rodriguez 1987). To date, the only important taxonomic difference between these two taxa has referred to the possession of elongated hair setae in segment III in *P. longiseta*; in *P. proboscidea* the hair setae of this segment are as long as those of the neighbouring

segments. Typically, the hairs of both *P. longiseta* and *P. proboscidea* are serrated, but the elongate hairs of *P. longiseta* are normally smooth. Sometimes, however, the setal characteristics of *P. longiseta* overlap with those of *P. proboscidea*. In African material, Grimm (1990) found (1) specimens with elongate, smooth hair setae in segments II and III; (2) a large variation in the serration of the hair setae (even the elongate hairs in segment III were sometimes serrated), which has been used to separate subspecies in *P. longiseta* (Sperber 1948: 237; Brinkhurst and Jamieson 1971: 403); and (3) specimens in which only the hairs of III, or those of both II and III, were reduced in length or even completely lacking, i.e. animals that according to an identification key would be *P. proboscidea*. Absence of elongate hairs may in some cases be due to loss, probably in handling the specimens. Because of these taxonomic uncertainties, Grimm (1990) did not include *P.*

proboscidea in the list of African naidid species. Its possible African occurrence has been based on a single individual found on Zanzibar (Michaelson 1905), but the affiliation of this specimen with *P. proboscidea* is more than doubtful. On the basis of setal morphology, the question may even arise whether *P. proboscidea* is merely a variety of the widespread *P. longiseta* with reduced hair setae in segment III.

However, the present material of *P. proboscidea* has revealed that the genital organs are different in the two taxa. In *P. longiseta*, the atria are clearly wider and have thicker walls than the vasa deferentia, and although the epithelia of both the atria and vasa deferentia are glandular, prostate glands are nowhere present (Piguet 1906: Figs 22, 24–25; Sperber 1948). This differs considerably from the slender, thin-walled atria, and heavily prostatic vasa deferentia in *P. proboscidea* (Fig. 3B). Furthermore, in *P. longiseta*, the spermathecae are not small

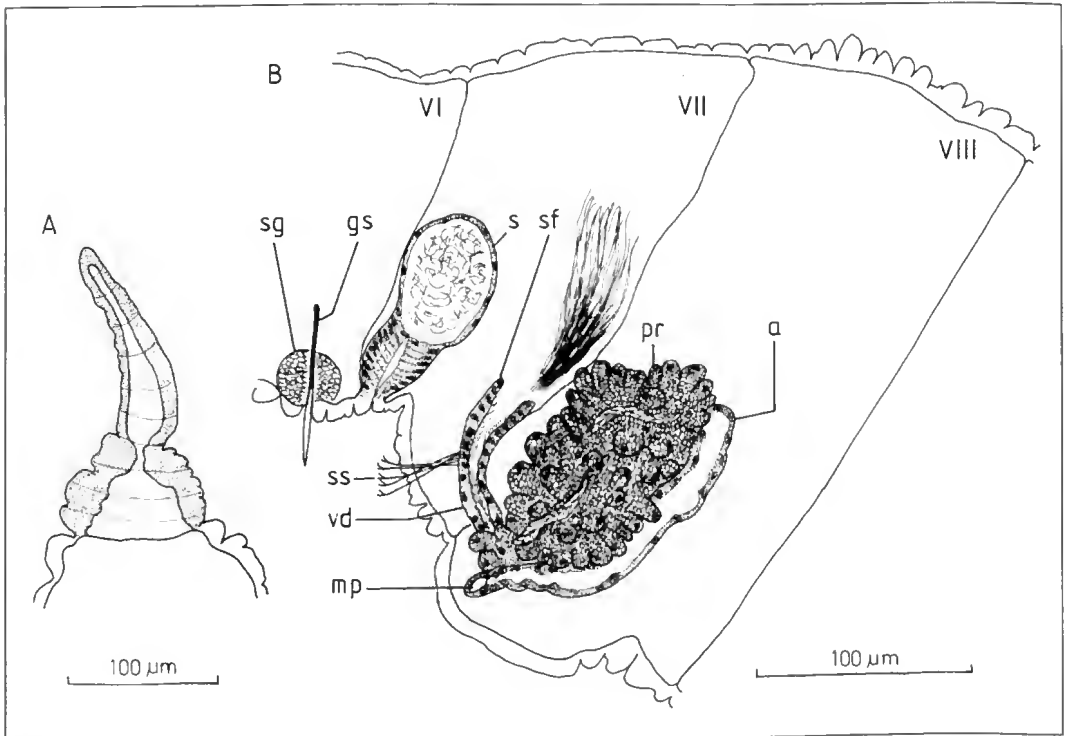


Fig. 3. *Pristina proboscidea*. A, prostomium with proboscis; B, lateral view of segments VI–VIII, showing genital seta, spermatheca and male duct of one side of worm. Abbreviations: a, atrium; gs, genital seta; mp, male pore; pr, prostate gland; s, spermatheca; sg, setal gland; ss, somatic seta; sf, sperm funnel; vd, vas deferens.

and club-shaped (as in *P. proboscidea*; Fig. 3B), but long, with ampullae extending through the whole length of segment VII (Piquet 1906: Figs 22, 25). Finally, Piquet reported that, in *P. longiseta*, the glands associated with the genital setae in VI do not envelop the setae but are situated separate from and behind these setae (Piquet 1906: Figs 22, 25).

With regard to the prostatic vasa deferentia and the slender, thin-walled atria, *P. proboscidea* resembles *P. americana* Cernovitov, 1937 (Cernovitov 1937: Fig. 10) more closely than *P. longiseta*.

Distribution. To date, *Pristina proboscidea* has been recorded from North (Brinkhurst 1986) and South America (Harman *et al.* 1988), South (Ali and Rashiduzzaman 1976) and East Asia (Brinkhurst *et al.* 1990), Australia (Pinder and Brinkhurst 1994; present paper) and New Zealand (Bayly 1989). Its occurrence in continental Africa is less certain (see above), but it has been reported from the irrigation system of Tenerife (Grimm 1978). A record from the Iberian Peninsula (Rodríguez and Armas 1983) is the only known European occurrence so far. The species thus appears widespread, but it may not be cosmopolitan. Rodríguez (1987) considered the special geographical situation of the Iberian Peninsula to favour recent introductions of American naidid species. This could apply also to Tenerife.

Pristinella osborni (Walton, 1906)
(Figs 2, 4)

Material studied. NTM Wo 0128, 1 whole-mounted specimen from small freshwater creek feeding into Stephens Creek, West Arm, Darwin Harbour, Northern Territory, Australia, 12°38'S, 131°43'E, sand with roots and debris along a short stretch of pools and rapids; coll. C. Erséus, 15 July 1993 (CE station no. 35).

Description. Length (contracted) 1.9 mm. Sexually mature specimen without budding-zone, with 26 segments. Prostomium without proboscis, rounded. Clitellum not developed. Dorsal setae: hairs one per bundle, smooth; needles, one per bundle,

bifid with nodulus at half to one third from distal end. Teeth of needles clearly visible, equally long (about 2.5 µm) and diverging at a wide angle (Fig. 2C). Needles 39 µm long in II, 34 µm in III, decreasing towards 30 µm in posterior segments. Ventral setae four to five per bundle in II, five per bundle in III–IV, six per bundle in V, one per 'bundle' in VI–VII, four per bundle in VIII, then decreasing to three per bundle posteriorly. Most anterior ventrals with distal tooth slightly longer than proximal, and nodulus proximal; posterior ventrals with equally long teeth and nodulus median to slightly distal (Fig. 2A). Ventral setae not measurable in anterior segments; setae more than 32 µm long, decreasing to about 30 µm in the posterior segments. In segments VI and VII, genital setae modified, about 60 µm long, without nodulus, bifid with prolonged straight, parallel, teeth comprising one third of setal length (Figs 2B, 4: gs). Each genital seta associated with large gland (Fig. 4: sg) histologically resembling prostate glands. Male and spermathecal pores paired, in line with ventral setae; male pores somewhat anterior to middle of VIII, spermathecal pores immediately posterior to furrow between VI and VII.

Pharyngeal glands in III–V. Coelomocytes numerous, spherical, about 5–10 µm wide, each with distinct nucleus surrounded by weakly granulated cytoplasm. Stomachal dilatation not distinct. Male genitalia (Fig. 4) paired. Sperm funnel indistinct, but revealed by adhering spermatozoa. Male duct a continuous, ciliated, tube, at least about 180 µm long, about 10–12 µm wide; transition between vas deferens and atrium not obvious. Proximal part of duct naked, middle part surrounded by continuous mass of tightly packed, heavily granulated, prostate cells. Distal part of male duct naked and terminally opening to exterior through inconspicuous pore. No part of male duct with any notable muscular layer. Spermathecae (Fig. 4: s, so) small and club-shaped, each with somewhat bulbous duct, about 20 µm long, about 15 µm wide, and oval ampulla, 30–35 µm long, about 25 µm wide. Spermathecal ampullae containing spermatozoa, somewhat loosely arranged in small bundles.

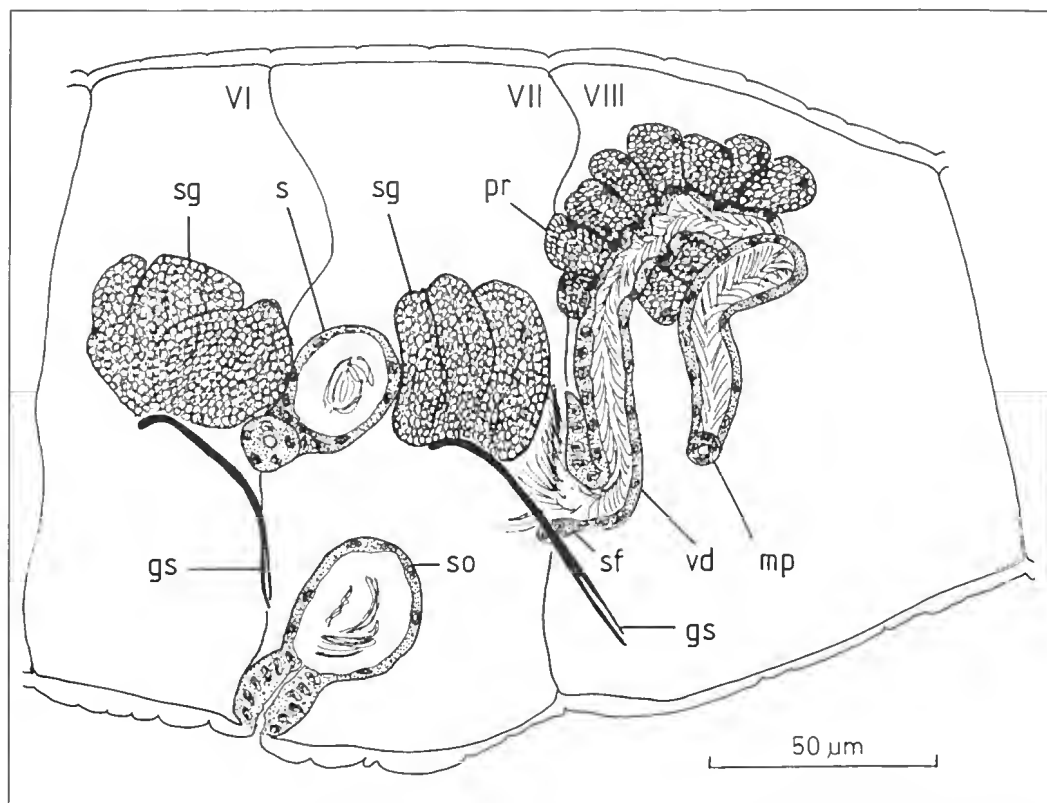


Fig. 4. *Pristinella osborni*, somewhat obliquely lateral view of segments VI–VIII, showing genital setae and male duct of one side of worm, plus spermathecae of both sides. Abbreviations: gs, genital seta; mp, male pore; pr, prostate gland; s, spermatheca; sf, sperm funnel; so, spermatheca of other side; vd, vas deferens.

Remarks. This species, one of the smallest naidids known, was first described by Walton (1906), as *Naidium osborni*, from Ohio, North America. Stephenson (1914) described *Naidium minutum* from Lahore, India. Sperber (1948) placed both species in the genus *Pristina* as *P. minuta* Stephenson, 1914. Brinkhurst and Jamieson (1971) stated that the separation of *Naidium osborni* from *N. minutum* was based on such slight differences that it had to be neglected, and correctly used the oldest name, *Pristina osborni* (Walton, 1906). Following Brinkhurst (1985), it is now called *Pristinella osborni* (see Discussion).

The new specimen fits the description given by Sperber (1948). Its needle setae are simply bifid and not pectinate. Intermediate teeth as reported by Grimm (1990) and Pinder and Brinkhurst (1994) are not visible (very few needle setae are in a suitable position for detailed observation).

According to Brinkhurst and Jamieson (1970), there should be a sudden stomachal dilatation in VII or VIII, but none is visible in the present material.

As described above, each male duct of *P. osborni* is a ciliated tube without a clear demarcation of an atrium, and it is not conclusive whether or not a proper atrium (an invaginated, ectodermal, part of the male duct) is present.

Distribution. *Pristinella osborni* appears more or less cosmopolitan. It is the most abundant *Pristinella* species in Europe, where it is often found in freshwater meiobenthos and in groundwaters. It has been reported from southern Europe (Martínez-Ansemil 1984; Sambugar 1986) up to the River Rhine basin in the north (Lafont and Durbee 1990; Wiegand and Matthess 1993). In America, the northernmost report comes from Lake Erie (Spencer 1977), the southernmost from

Bolivia (Juget and Lafont 1994). It is also recorded from Africa (Grimm 1990), Asia (Naidu 1961) and Australia (Pinder and Brinkhurst 1994; present paper).

DISCUSSION

Pristina Ehrenberg, 1828, and *Pristinella* Brinkhurst, 1985, originally treated as a single genus (*Pristina*), are currently the only genera in the subfamily Pristininae *sensu* Sperber (1948), a taxon subsequently revised to become a tribe, Pristinini, within the Naidinae (Nemec and Brinkhurst 1987). This group is 'curiously homogeneous' (Sperber 1948: 247), differing from all other Naididae by (1) its dorsal setae commencing from segment II, (2) its continuously tubular male duets, and (3) the relatively high number (seven as opposed to four to five) of segments formed at the anterior end in a budding zone. At least the first two of these features may be plesiomorphic, but for the sake of the following discussion it is assumed that the Pristininae/Pristinini are monophyletic. Sperber's (1948) description of the Pristininae also mentions 'the characteristic stomach, with cells containing intra-cellular canals with special features', but these canals were not observed in the present material. As pointed out by Brinkhurst (1985), they need to be re-investigated using electron microscopy.

Brinkhurst (1985) separated *Pristinella* from *Pristina sensu stricto*, referring to a number of morphological differences. According to him, *Pristina* is characterised by a prostomial proboscis, genital setae in at least two different segments (varying positions), presence of spermathecae, and prostate glands on the vasa deferentia, whereas in *Pristinella*, proboscis, prostate glands and spermathecae are absent, and genital setae are either absent, or present in VIII (based on the genital organs of only two species, *Pristinella amphibiotica* (Lastockin, 1927), and *P. idrensis* (Sperber, 1948)). *Pristina proboscidea* fits into this general pattern, whereas *Pristinella osborni* does not. The latter possesses spermathecae as well as prostates, and it has genital setae in both VI and VII, but not in VIII (see Fig. 4).

Thus, with regard to genital features, *P. osborni* fits Brinkhurst's definition of *Pristina* better than that of *Pristinella*.

Pristina and *Pristinella* contain about ten species each, but they are often difficult to discriminate because of a wide overlap of taxonomic characteristics. Several additional nominal species in the literature are regarded as dubious (e.g., four species described by Botca 1983) or as junior synonyms of other taxa.

The male duets are now known for six of the *Pristina* species: *P. longiseta* (type species), *P. breviseta* Bourne, 1891, *P. plumaseta* Turner, 1935, *P. leidy* Smith, 1896, *P. americana* and *P. proboscidea*. The atria are generally slender (short in *P. plumaseta*), and when present, the prostate glands are associated with the vasa deferentia, not with the atria. Prostates have not been observed in *P. longiseta* and *P. leidy*, but the inner ends of the male duets have somewhat glandular walls in these two species (Piguet 1906; Smith 1896).

For the taxa currently placed in *Pristinella* (see Brinkhurst 1985), information on male duets is scanty. According to Sperber (1948), *Pristinella amphibiotica* and *P. idrensis* have short vasa deferentia followed by atria that are either 'not differentiated' or 'small'; prostate cells are 'probably' absent. In his description of '*Pristina amphibiotica changmuensis*', Liang (1963: fig. 2F) illustrated a more developed and differentiated atrium, the male duet, however, still lacking prostate glands. *Pristinella osborni*, on the other hand, has prostate glands along the middle part of its male duets but lacks demarcated atria (Fig. 4). In fact, as the male duets of *P. osborni* are ciliated throughout, this species may lack atria altogether; Sperber (1948: 49) claimed that naeid atria are non-ciliated. The previously studied material of *P. amphibiotica* and *P. idrensis* were possibly not as sexually mature as the present individual of *P. osborni*, which could explain why prostate glands and spermathecae were not observed in the two former taxa. Alternatively, *P. osborni* could be regarded as representing a third (yet un-named) genus in the *Pristina/Pristinella* complex. At any rate, the distinction between *Pristina* and *Pristinella* does not appear as clear as it was initially thought to be (see Brinkhurst 1985).

A prostomial proboscis does not occur only in *Pristina*, but also in the other naidid genera *Stylaria* Lamarck, 1816, *Arcteonais* Piguët, 1928, and *Ripistes* Dujardin, 1842, and *Homochaeta* Bretscher, 1896 (Grimm 1985). The phylogenetic analysis by Nemec and Brinkhurst (1987), however, indicates that the three latter taxa are not closely related to the *Pristina/Pristinella* complex. The (synapomorphic) possession of a proboscis thus appears to support monophyly of *Pristina sensu stricto*, i.e., assuming that the absence of a proboscis in *Pristinella* is not the result of a secondary loss of this character.

The observations on the present material elucidate the importance of including genital features in assessments of naidid morphology and phylogeny. Much work remains until the phylogenetic relationships within the *Pristina-Pristinella* complex, as well as within the Naididae as a whole, are resolved.

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Accepted 28 October, 1997

DESCRIPTION OF *ARICHLIDON* NEW GENUS AND TWO NEW SPECIES
FROM AUSTRALIA; *BHAWANIA REYSSI* REDESCRIBED AND ASSIGNED
TO *ARICHLIDON* (CHRYSOPTALIDAE: POLYCHAETA).

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ABSTRACT

Arichlidon hanneloreae gen. nov., sp. nov. is described from coastal and offshore coral reefs in tropical eastern and western Australian waters, Papua New Guinea, Indonesia and the Marshall Islands. *Arichlidon acropetalon* sp. nov. is described from deeper waters off north Queensland, eastern Australia. *Bhawania reysi* Katzmann, Laubier and Ramos, 1974, is redescribed and assigned to the new genus *Arichlidon*. Additional material of *B. reysi* is recorded from Cape Verde Islands, Eastern Atlantic; Mediterranean localities, including specimens from abyssal depths of the eastern Mediterranean, and the Red Sea. The new genus is characterised by a distinct convex, broad, short body form and the shapes of the highly ornamented lateral, main and median paleae groups. Epitokous spinigerous neurosetae, not recorded before in the Chrysopetalidae, are described for *Arichlidon hanneloreae* sp. nov..

KEYWORDS: Polychaeta, Chrysopetalidae, *Arichlidon*, new genus, new species, Australia, Indo-West Pacific, Mediterranean

INTRODUCTION

Species belonging to this chrysopetalid group have been recognised as problematical for some time. Laubier (1966) first recorded specimens from the waters off Beirut as 'Chrysopetalidae gen. sp.?' Ramos (1973) later described specimens from the French and Spanish Catalan coasts as '*Heteropale* ?sp.' in her dissertation. Katzman, Laubier and Ramos (1974) then collaborated to describe a new species from the Adriatic, *reysi*, provisionally placed in the genus *Bhawania*. Perkins (1985) recognised material from Florida waters as belonging to a new genus and species and in his key to the Chrysopetalidae referred specimens to "*Bhawania reysi*" [sic]. Watson Russell recognised eastern and western Atlantic and Mediterranean specimens as belonging to the same new genus, in a paper given at the First International Polychaete Conference, Sydney, Australia, (1983) and made reference to this material in a number of publications as 'new

genus 1' (Watson Russell 1986, 1987, 1991).

Material examined is in the following institutions: Australian Museum, Sydney (AM); Hebrew University Zoological Museum (HJ); Los Angeles County Museum (LACM); Muséum d'Histoire Naturelle, Paris (MNHN); National Museum of Natural History, Washington (USNM); Museum of Victoria (NMV); Naturhistorisches Museum, Wien (NMW); Queensland Museum (QM); Museum and Art Gallery of the Northern Territory (NTM); Senckenberg Museum, Frankfurt (SMF).

Setal terminology follows that of Watson Russell (1986, 1991). Setal counts, unless otherwise indicated, are taken from mid body segments. In the generic description, the setal count given is the most common range taken overall from a large number of individuals (very occasional higher counts are indicated in brackets). In the species descriptions the setal counts from the holotype are given first; those for additional material are enclosed in brackets.

SYSTEMATICS

Family Chrysopetalidae Ehlers, 1864
Genus *Arichlidon* gen. nov.

Type species. *Arichlidon hanneloreae* sp. nov., by original designation.

Diagnosis. Relatively short, broad body form; prostomium with two pairs violet-black eyes often fused, forming rectangular block visible beneath paleae of anterior segments. Lateral paleae fascicle intergrading smoothly with main paleae fascicle; distinctive group of asymmetrical, ornate median paleae interlocking at mid-dorsal line forming smooth convex ridge. Falcigerous inferior neurosetal blades, short, broad, non-dentate, curved with blunt tip.

Description. Body rectangular, broad, slightly tapered at both ends. Juveniles ovoid in shape. Maximum segment number 55. Body white to pale brown. Silver to gold coloured paleae fans, often flecked with brown scale, imbricate over dorsum, covering worm completely. Paleae in transverse row in notopodium with leading edges visible proximally; median paleae interlocking at mid-line, forming distinct convex median ridge. Broad notosetal fans extending entire width of dorsum; neuropodia tucked behind notopodia, only visible ventrally.

Anterior three segments in conjunction with prostomium largely retractable. Prostomium small, oval, compressed between anterior segments. Two pairs of large, violet-black eyes on dorsal surface of prostomium; eyes often fused to form solid pigmented rectangle. Single, large, subulate median antenna inserting anterior to anterior pair of eyes; two slightly longer lateral antennae inserting on antero-ventral margin of prostomium. Two long cylindrical palps inserting on ventral edge of prostomium. Triangular mouth fold ventral and posterior to palps; eversible proboscis with two transparent, distally serrate stylets. Semi-circular glandular nuchal fold present posterior to, and capable of covering, prostomium.

Segment 1 reduced, fused in part to prostomium; supporting a dorsal and ventral tentacular cirrus on each side; ventral pair

originating adjacent to palps. First setigerous segment (segment 2) biramous, fused in part to segment 1; notopodium with small number of short paleae and dorsal cirrus; small neuropodium directed anteriorly with fascicle of spinigerous neurosetae; ventral cirrus absent. Short paleae of notopodia, segments 2-4, often including rounded primary (larval) paleae types. Segments 3 and 4 directed antero-laterally; all subsequent setigers directed laterally. All setigers except first with three types of paleae, dorsal and ventral cirri, spinigerous and falcigerous neurosetae. Interramal region ciliate; a number of ciliate tufts posterior to paleae fan insertion.

Notopodium with three to seven subacicular lateral paleae with 6-17 ribs. Lowermost lateral palea symmetrical, small, pointed, with finely serrate upper margin and finely serrate distal third of lower margin, with one finely raised rib, granules absent; uppermost lateral palea, larger, slightly asymmetrical, with serrated margins and raised ribs. Tiny, serrate, simple seta usually present, posterior to overlying, dorsal acicula. Large group of broad, symmetrical main paleae with 13-22 ribs and one to eight raised and highly ornate ribs. Medial-most main palea (subunit 1) may be similar size and shape as other main paleae or taller, or broader and asymmetrical, with up to six raised ribs; present mid to posterior body. Narrow fascicle of four to six median paleae originating at angle to main fan. Each median palea grading in size and degree of acute asymmetry within fan. Lateral-most palea largest with outer margin straight, inner margin acutely bent and 11-18 ribs; this palea may be shorter, same size or taller than paleae of main fan. Mid-median group with 10-14 ribs; medial-most palea smallest, near symmetrical, pointed with 7-10 ribs and no raised ribs or granules. All other median paleae with one to four, usually three raised ornamented ribs. Subunit 2 palea slender, symmetrical with 8-11 ribs, two finely raised ribs, equally serrate margins present within median fascicle in posterior half or posterior-most segments of body. Large granules dense, scattered or absent on superior surface of majority of paleae types; paleae margins strongly serrate; close-set horizontal

striae between longitudinal ribs continuing to distal end of paleae; paleae terminating distally in distinctly elevated, shallow or sunken apex. Long, slender, subulate, slightly pseudoarticulated dorsal cirrostyle, often concealed behind paleae fan. Dorsal cirrophore and cirrostyle up to twice as long in posterior setigers, extending past pygidium.

Short, pointed neuropodia not extending past notopodia and supporting a subacicular fascicle of heterogomph neurosetae. Very slender, fine simple seta overlying ventral acicula, often visible extending past neuroacicula tip. Superior group of 1-3(5) spinigers with long slim shafts and fine attenuated blades with fine basal teeth. One extra or replacement subunit 1 short spiniger present within posterior segments. Mid-superior group of 2-6(8) falcigers with long blades in upper position, medium-length blades with robust basal teeth below. Mid-inferior group of 6-15(20) falcigers with medium to short-length blades with basal teeth. Inferior group of 6-10(15) falcigers with short broad blades with few to no teeth, terminating in blunt curved tip. Dentition on blades extending full length of blade stopping just before curved tip; last denticle forms opposing tooth to tip. Epitokous spinigers numbering 1-14 may be present in superior position of ventral ramus; spinigers composed of long to very long, slender shafts with almost homogomph joints and long, attenuated blades. Ventral cirri slender, weakly pseudoarticulated and a little shorter than dorsal cirri. Pygidium composed of rounded to quadrate dorsal structure with two short or long anal cirri, and a long ventral glandular cone.

Remarks. *Arichlidon* differs from all other chrysopetalid genera in possessing a relatively short, broad body form, a lateral paleae fascicle that intergrades with the main paleae fascicle and a distinctive group of asymmetrical ornate median paleae that interlock at the mid-dorsal line forming an arched smooth convex ridge (Fig. 1A-B). The shape of the falcigerous inferior neurosetal blades, short, broad, non dentate and curved with a blunt tip, are diagnostic of the genus (Fig. 3G-I). Another distinguishing character is the arrangement of the violet-

black eyes.

The formula of cirri on the anterior segments of *Arichlidon* is the same as that found in the majority of chrysopetalid genera - *Strepternos*, *Paleanotus*, *Hyalopale*, *Treptopale*, *Paleaequor*, and *Bhawania*. The semi-circular nuchal fold of *Arichlidon* is similar to that seen in *Paleanotus*, *Treptopale*, *Paleaequor* and *Strepternos*.

Arichlidon species have previously been confused with those of *Bhawania* and *Paleanotus*. *Arichlidon* and *Bhawania* are distinctly different genera with the latter having a long rectangular body form of 100 plus segments covered in golden brown paleae and possessing different numbers and types of notosetae and neurosetae.

Paleanotus, *Hyalopale* and *Treptopale* form a closely related group within the Chrysopetalidae; the former two genera possess distinctly asymmetrical main paleae types distinguishing them from *Arichlidon*. *Treptopale* has ornate, symmetrical main notosetal types very similar to those of *Arichlidon* but both genera possess differently shaped appendages of the anterior segments, different pygidial forms and numbers and types of notosetae, especially the median group. The main paleae of *Arichlidon* insert with leading edge facing the medial dorsal line, whereas in *Treptopale* the leading edge faces out towards the lateral line.

The ornate, symmetrical main paleae found in *Arichlidon* are also seen only in the larvae and juveniles of the deep sea chrysopetalid genus *Strepternos* (Watson Russell 1991). The small neuropodial simple seta, seen in *Arichlidon* adults (Fig. 3A), is found in juveniles and then lost in adults in the majority of other chrysopetalid genera. Some *Dysponetus* species, most likely neotenous forms, retain larger neuropodial simple setae. The tiny notopodial simple seta seen in *Arichlidon* adults (Fig. 1A) is also found in juveniles of other genera (Watson Russell 1986).

The shape of the two slender stylets is similar to those found across all chrysopetalid genera (Fig. 2C). The shape of the mouth fold and the robust, distally serrate stylets are most similar to those belonging to *Chrysopetalum* species. Two

specimens of *A. hanneloreae* were found to have the proboscis everted; in one specimen the stylet tips were just visible, in the other they were extended out half their length.

Arichlidon species are recorded from many crevicular habitat types, some of which are associated with sessile invertebrate animals eg tube dwelling polychaetes, tube dwelling amphipods and inside bivalve molluscs. It is possible that *Arichlidon* species are both scavengers and active predators on these invertebrates.

Arichlidon species can be found in large numbers in preferred habitats. *Arichlidon* species have been recorded across a broad range of habitat types, from tropical to temperate waters, world wide between 40° N and 39° S. They are found in seagrass, algal, sponge, hydroid and shell habitats, crevices in coral and rocky reefs, rotting wood in mangrove channels, and from every grade of sand, clay and mud substrate in warm shallow waters to the edge of the continental shelf and beyond to abyssal depths. Depths in which they are found range from the intertidal to 3947 m.

Etymology. The name *Arichlidon* is a combination of the Greek *ari*, meaning "highly", and *chlidon*, meaning "ornamentation", and refers to the raised ribs sculptured with large cusps down the length of the superior surface of paleae. Gender neuter.

Key to *Arichlidon* species

- 1a. Mid-body segments with lateral-most median palea the tallest palea in fan (Fig. 4C) 2
- 1b. Mid-body segments with lateral-most median palea not the tallest palea in fan (Figs 1C, 4A-B) *A. hanneloreae* n. sp. (Australia, Indo-West Pacific)
- 2a. Main paleae with distinct broad 'shoulders'; small elevated apices and granules (Fig. 6G-H)... *A. reyssei* (Eastern Atlantic, Mediterranean, Red Sea).
- 2b. Main paleae with distinct rounded 'shoulders', large elevated apices, granules absent (Figs 5A-B, 6E-F) *A. acropetalon* n. sp. (North Queensland, Australia).

Arichlidon hanneloreae sp. nov.

(Figs 1A-D, 2A-D, 3A-J, 4A-B, 6A-D, I-J)

Bhawania cryptocephala non Gravier - Hartman, 1954: 628.

Type material. HOLOTYPE - Australia, Queensland, Townsville, Halifax Bay, Stn.79-2A-14, sediments near coral reef, 2 m, coll. J. Carey, February 1979, 1, NTM W1563, length 3.7 mm, width 0.92 mm, 33 segments entire; PARATYPES - 3, same data as holotype. Length 2.4 mm, width 0.8 mm, 28 segments entire; length 2.1 mm, width 0.75 mm, 20 segments entire. 2, NTM W1564; 23 segments, near entire; 1, BMNH ZB1985.81.

Additional material. (Selection). VICTORIA, Western Bass Strait, Stn. 71, 39° 22' 2" S, 143° 10' 1" E, medium fine sand, 101 m, 10 October 1980, coll. G.C. Poore, HMAS *Kimbla*, 1, NMV F82.902. TASMAN SEA, Lord Howe Island, Balls Pyramid, 31° 46' S, 159° 16' E, dredged, 91-183 m, coll J. MacIntyre, CSIRO Fisheries, 22 November 1960, 1, AM W23231; Middleton Reef, 29° 27' 4" S, 159° 03' 7" E, Site 8, outer slope near *Runic* wreck, dead coral and algae in surge channels, 15 m, coll. P.A. Hutchings, 5 December 1987, 2, AM W23370; Elizabeth Reef, 29° 57' 2" S, 159° 01' 2" E, outer slope west of *Yoshin Maru Iwaki* wreck, 12 m, coll. P. Hutchings, 10 December 1987, 1, AM W23358. QUEENSLAND, Gladstone, Site 4, mud, 12 m, dredge, coll. W.S., 6 November 1975, 1, QMH 615; Heron Island, reef pool, 12 July 1983, coll. W. Westheide, 6 November 1975, 1, NTM W13189; Low Isles, coral rubble washings, 6-8 m, coll. C. Watson Russell, 22 December 1987, 2, NTM W13186; Lizard Island, Chinamans Head, 14° 36' S, 145° 38' E, Stn. 76 Liz B06.12.3, reef rock, coll. P. Hutchings and P. Weate, 8 January 1977, 2, AM W23237; same locality, substrate and collectors as previous, Stn. 76 Liz B06.12.2, 8 December 1977, 1, AM W23236; near Bird Islet, 14° 36' S, 145° 38' E, Stn. 76 Liz A12.24.3, reef rock, same collectors as previous, 22 January 1978, 5, AM W23234; grid on reef floor on windward outer slope between Bird Islet and South Island, Stn. 76 Liz A00.09.2, 12m, coll. P. Hutchings, 1, NTM W13191; Outer

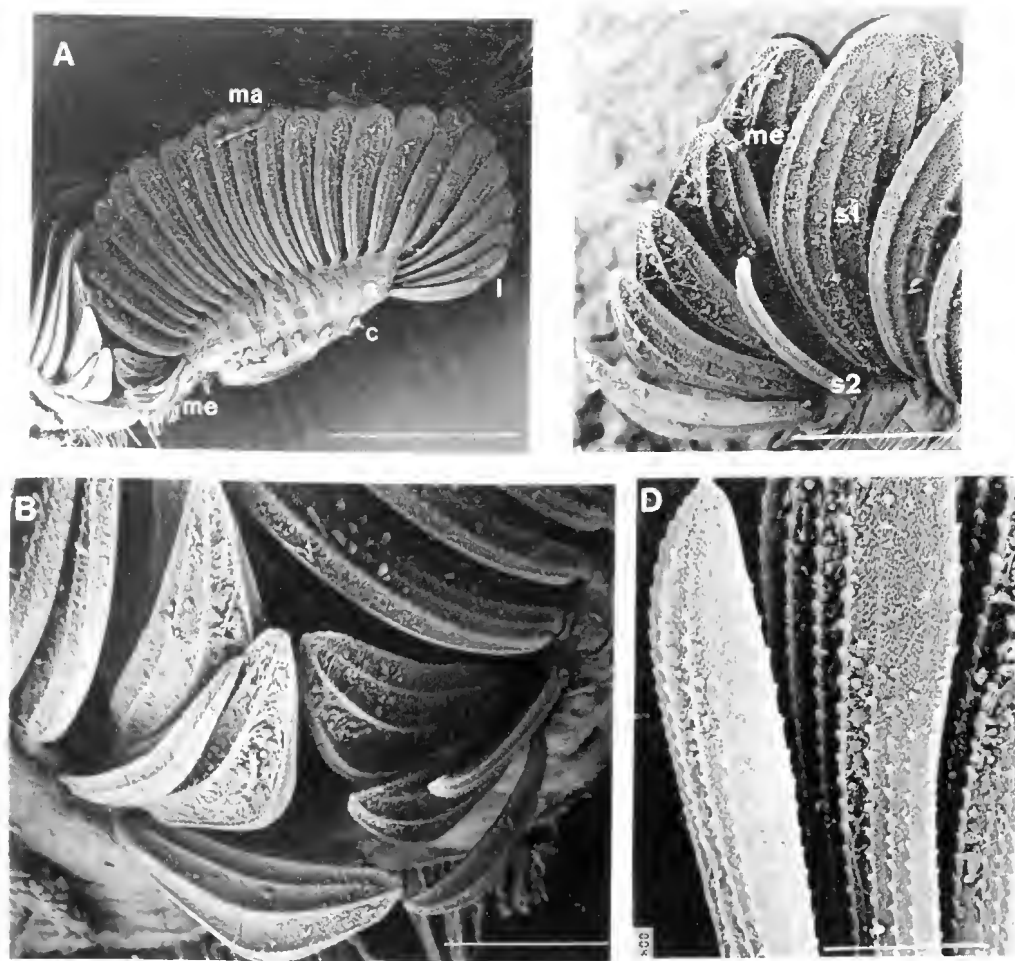


Fig. 1. Scanning electron micrographs. **A-B**, *Arichlidon hanneloreae*, LACM n. 10164. **A**, mid body notopodium; **B**, close up of median paleae group. **C-D**, *A. hanneloreae* AM W23231. **C**, mid body, notopodium in part, median paleae group; **D**, detail of raised ribs and granules of main paleae. Abbreviations: **l**, lateral sub-acicular paleae group; **ma**, main paleae supra-acicular group; **me**, median paleae group; **s1**, subunit 1 palea (medial most main); **s2**, subunit 2 palea; **s**, tiny dorsal simple seta, **c**, cilia tuft. Scale: **A**= 250µm; **B-D** = 50µm.

Yonge Reef, 14° 36' S, 145° 28' E, Stn. 77 Liz 53-1, *Halimeda* covering coralline pink algae, 20 m, coll. P. Hutchings and P. Weate, 21 January 1977, 5, AM W23209; north-west of Lizard Island, Cooks Passage, Cod Hole, 14° 31' S, 145° 34' E, reef rock, 10 m, 4 September 1995, coll. A. Murray, 1, AM W23207. NORTHERN TERRITORY, Gulf of Carpentaria, 15° 21' 47" S, 136° 31' 13", Bing Bong, Stn. T7A, 14-17m, September 1992, coll. J. R. Hanley *et al.*, 1, NTM W13143; Gove, Melville Bay, Stn. A15W, 4 m, sand and little mud, 19 March 1992, coll.

J. R. Hanley *et al.*, 2, NTM W13026; Weed Reef, Darwin Harbour, 12 m, silt, coarse sand and shell, coll. P. Horner, 2, NTM W2052; Central Darwin Harbour, Stn. D61A, 3 m, gravel, coarse sand, 7 July 1993, coll. J. R. Hanley *et al.*, 1, NTM W13119. WESTERN AUSTRALIA, off Broome, 16° 33' S, 121° 29' E, Stn. 85-2, 40 m, beach coralline rock with sponge growth, coll. B.C. Russell, pair trawl, 17 April 1985, 2, NTM W2933; Ashmore Reef, NW end, outer reef slope, coralline algae and coral rubble washings, 15 m, 23 February 1984, coll B.C.

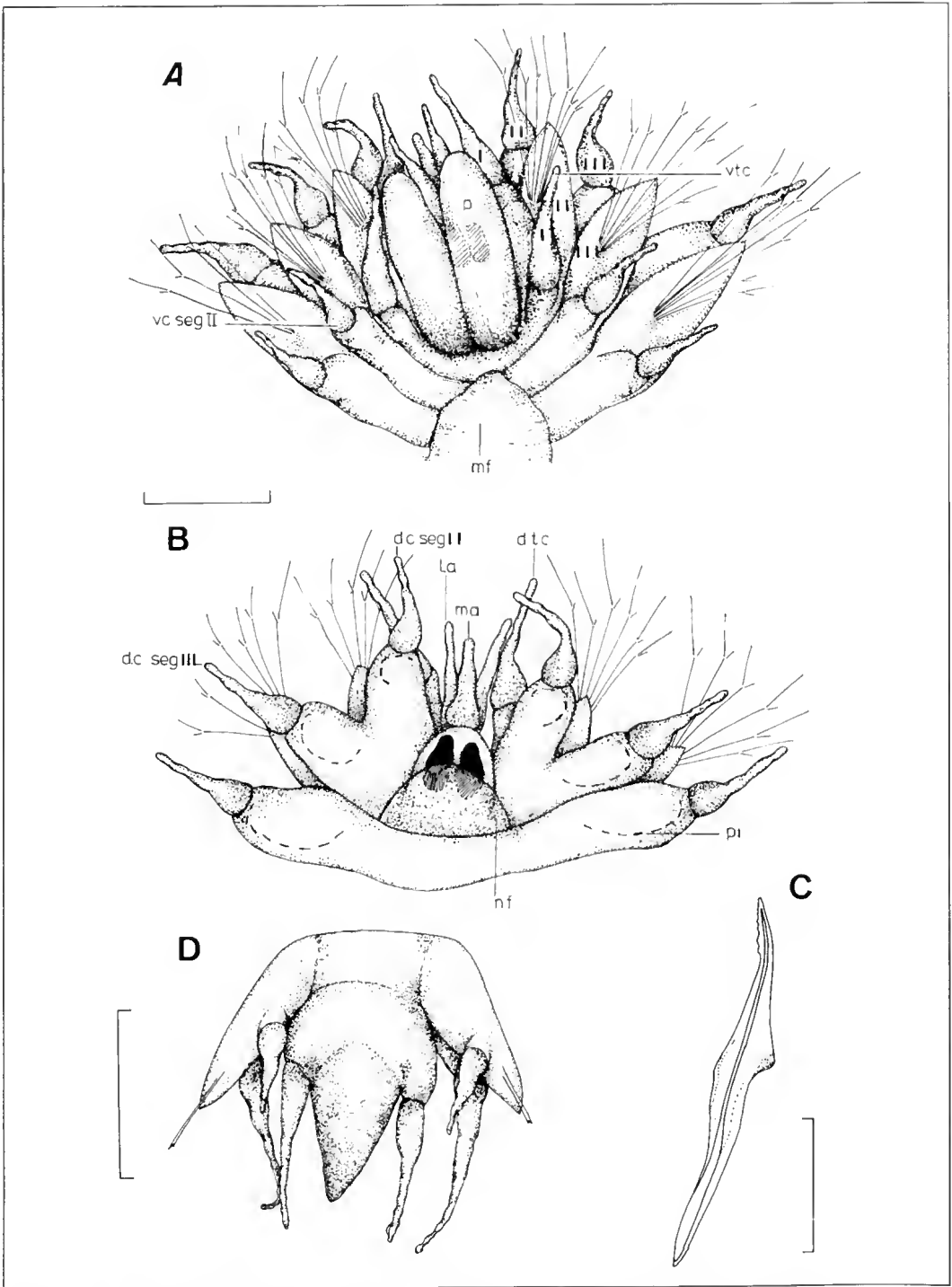


Fig. 2. A-B. *Arichlidon hanneloreae*, NTM W.1564. **A.** anterior end, ventral view. Abbreviations: **mf**, mouth fold; **p**, palp; **vte**, ventral tentacular cirrus; **vc seg. II**, ventral cirrus segment two; **I**, segment one; **II**, segment two; **III**, segment three; **B.** anterior end, dorsal view. Abbreviations: **ma**, median antenna; **la**, lateral antenna; **dte**, dorsal tentacular cirrus; **dc seg. II**, dorsal cirrus segment two; **dc seg. III**, dorsal cirrus segment three; **pi**, paleae insertion; **nf**, nuchal fold. **C.** *A. hanneloreae*, USNM 45381, stylet. **D.** *A. hanneloreae*, NTM W1564, pygidium, ventral view. Scale: A, B = 0.1 mm; C = 0.04 mm; D = 0.2 mm.

Russell, 1, NTM W9304; Imperieuse Reef, Rowley Shoals, dead coral and soft coral washings, 70 m, coll. B.C Russell, 1, NTM W9305; SW of Rowley Shoals, 19° 29.6' S (to 19° 29.5'), 118° 52.2' E (to 118° 52.7), Stn. 127, supernatant off echinoderms, 38 m, bottom trawl, 30 August 1983, 1, NTM W3704; NW Shelf, 19° 35' S, 115° 27' E, Stn. WP93/9B, locally cemented horizon with superficial sediments, 77 m, coll. Woodside Petroleum, 23 October 1993, 1, NTM W13092. PAPUA NEW GUINEA, Madang, Malamal, coral rubble and mud beds, 2-7 m, 25 October 1991, coll. J.R. Hanley, 2, NTM W7577; Madang, Sandy Bay behind Wongat Island, coral rubble in sand, 3-6 m, 19 October 1991, coll. J.R. Hanley, 7, NTM W7574. SOLOMON ISLANDS, Matiu Is., coral reef platform, LWM, coll. P.E. Gibbs, 7 August 1965, fragments, BMNH 1970-208. INDONESIA, Flores, Maumere, reef outside Sao Wisata, coral rubble and detritus, 5 m, 3 August 1987, coll. C. Watson Russell, 18, NTM W13185; same locality, coral rubble and encrusting fauna, 2.5 m, 2 August 1987, coll. C. Watson Russell, 7, NTM W13184; SW Sumatra, Sanding Island, Pulo Stupai, 3°26'S, 100° 40'E, December 1963, coll. A.J. Kohn on Te Vega Expedition, 1, USNM 45381. MICRONESIA, Marshall Islands, Eniwetok Atoll, Loc. 1519, coral reef, 1 m, coll. H.S. Ladd, 1, LACM (AHF) n. 10164.

Description. Description based on holotype with numerical information based on additional material in brackets. Holotype entire 33 segments. Anterior segments relaxed. Subulate median antenna visible on anterior edge of prostomium; two pairs of eyes visible above nuchal fold; two long cylindrical palps visible ventrally (Fig. 2A-B). Segment 2 (setiger 1) with five short paleae with 8-10 ribs. Segments 2-4 with two to three paleae types, usually including primary (larval) paleae types (Fig. 6I).

Subsequent body segments with notosetae comprising four to five (six to seven) lateral paleae; lower 2 with 6-11 (12) ribs, upper group with 10-14 ribs of which three to four (occasionally five) raised. Main paleae number 10-15 (19) with 14-16 (17, rarely 18, 19) ribs including four to seven raised ribs of which three to four extend full length of

palea. Most medial main palea (subunit 1), broad, asymmetrical with 16 (17, rarely 18) ribs and five to six raised ribs. This palea is first present about 15th segment, continues to most posterior segment; generally tallest palea in the fan, the same size or sometimes slightly smaller than largest median palea (Figs 1C; 4A-B). Median paleae number four to five, inner two with 8-10 (7-11) ribs, outer group with 11-13 (14-16, rarely 17) ribs; tallest median palea with 13 (14-16, rarely 17) ribs, most evident mid body. Subunit 2 symmetrical, slender, palea with seven to nine ribs of which two to three finely raised; coming in at mid body and continuing to end of body (Figs 4A; 1C). This palea not always present on all posterior segments and often difficult to see. Notopodia within posterior ten segments with smaller numbers of paleae, rounded lateral types, shorter, more slender median group (Fig. 6J).

Main and median paleae broad to very broad with small elevated to sunken apices, (juvenile specimens with remnant hoods), serrate margins, raised ribs with small serrated cusps, dense granulation on superior palea surface (Fig. 1D).

Neurosetae comprising superior group of one or two (three) spinigers with long slim shafts and attenuated blades (Fig. 3C); one extra or replacement short spiniger present within posterior setigers. Mid superior group comprising two to three long bladed falcigers in upper position (Fig. 3D) and four to eight medium length bladed falcigers below (Fig. 3E); all types with dentate blades. Mid inferior group of 6-10 (15) falcigers with shorter broader blades (Fig. 3G-H). Inferior group of 8-10 (15) falcigers with short broad blades (Fig. 3I); latter two groups of neurosetae with no dentition on blades. Pygidium composed of slender ventral cone and two anal cirri on dorsal pygidial structure (Fig. 2D).

Remarks. It is always important, where possible, to compare mid-body segments from similar sized specimens to determine species. Adult specimens of *Arichlidon haumeloreae* are distinguished from *A. reyssi* by possessing a tall medial-most main palea (= subunit 1 palea), nearly always the highest palea in the fan in mid-body

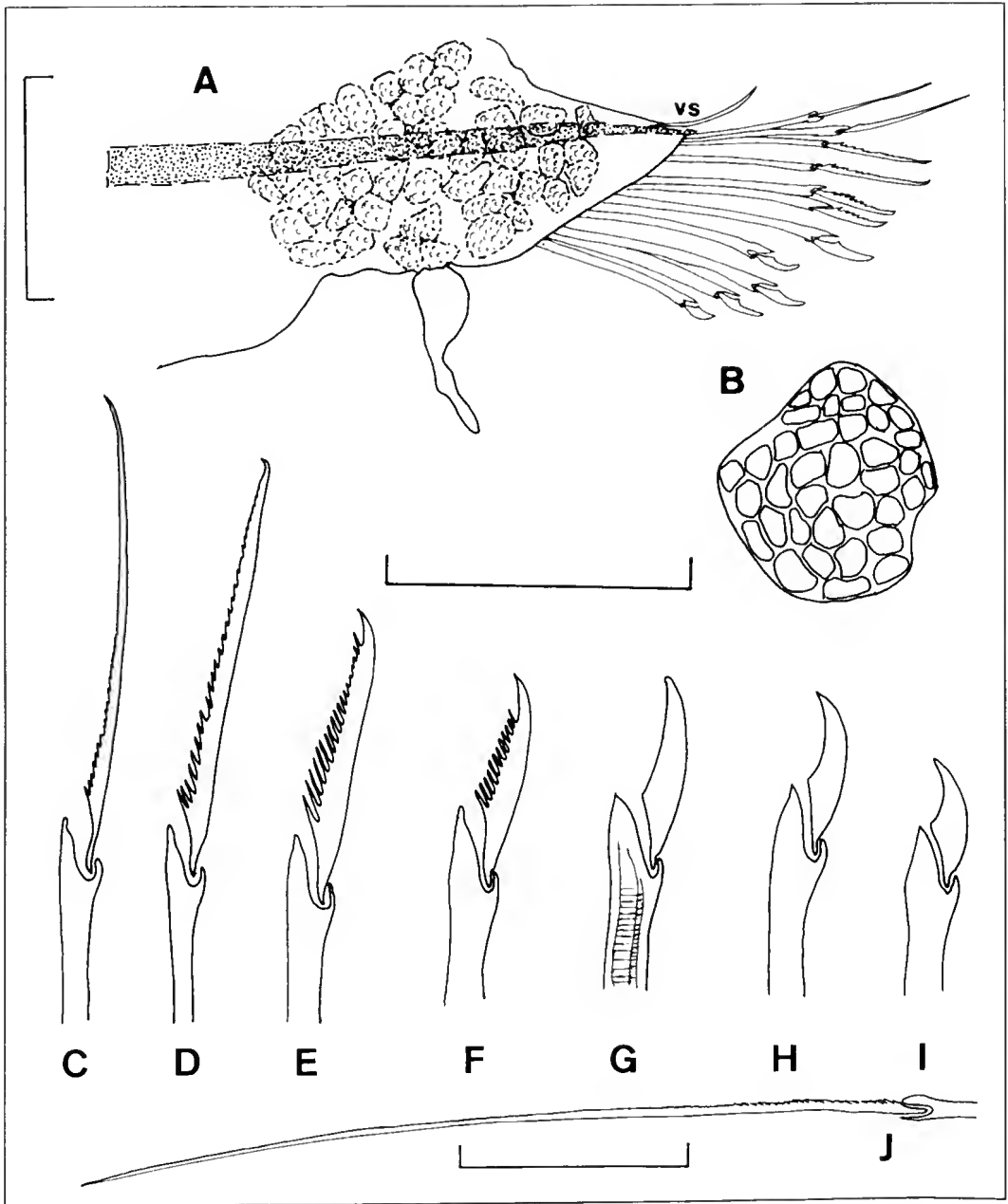


Fig. 3. *Arichlidon hanneloreae*, QM GH 615, female with eggs. **A**, neuropodium, segment 20, anterior view, v s, simple seta; **B**, detail of egg packet; **C**, superior spiniger; **D**, **E**, mid superior falcigers; **F**, mid inferior falcigers; **G-I**, inferior falcigers; **J**, epitokous spiniger. Note: epitokous spinigers not drawn in **A**. Scale: **A** = 0.1 mm, **B-J** = 0.04 mm.

segments (labelled S1 in Figs 1C, 4A). In *Ar. reyssi* the tallest palea in the fan in mid-body segments is the lateral-most median palea (palea labelled ME, Fig. 4C).

Three entire juvenile specimens of *Arichlidon hanneloreae* from Indonesia (9, 10 and 13 segments) all possessed four to five juvenile broad median paleae that are

distinctly shorter than the main paleae. In the 9 and 10 segmented material the large subunit 1 palea is present in the posterior most segments and in the 13 segment specimen from segments 8-13.

In posterior segments of a 13 segment specimen from Queensland the tallest median is shorter to the same size as the subunit 1 palea. It is clear that setal types are being replaced with growth and that the adult median paleae are present from around 13 segments and larger individuals. In two adult *A. hanneloreae* specimens the lateral-most median palea is the tallest in the fan in anterior segments and continues as the tallest or at the same height as the main paleae until segment 15 in 50 segments and segment 17 in 55 segments, when the the subunit 1 palea first is present.

In adult *Arichlidon hanneloreae* material in the mid-body, the subunit 1 palea predominates as the tallest palea in the fan especially when there are four median paleae in the fan (i.e. tallest median absent, Fig. 4A). When there are five median paleae (ie. tall median present), the subunit 1 palea may be taller (see Fig. 1C), the same size (Fig. 4B) or in some instances slightly smaller than the tall median. Between segments 15-45 of the dissected 50 segment *A. hanneloreae* specimen, 16 notopodia had the subunit 1 palea the same height, 10 had the subunit 1 palea taller and 4 the subunit 1 palea smaller than the lateral-most median.

In adults of *A. reyssi* the lateral-most median palea is the tallest palea in the fan in anterior segments and continues as such down the body. In a dissected 41 segment entire specimen of *A. reyssi* the adult lateral-most median palea comes in from segment 5 and predominates as the tallest palea in the fan until segment 35 (Fig. 4C). The subunit 1 palea is present from the 14th segment.

The small subunit 2 palea, which intergrades between the main and median paleae groups, is not counted as a median palea as it is often difficult to see or may be absent. The subunit 2 palea is present from midbody segments in both *A. hanneloreae* and *A. reyssi* species.

In this review all three *Arichlidon* species, possess similar anterior ends, pygidia and neurosetal types. Species differences are only

discernible between paleal notosetal shapes and lengths and their position in the body. The morphological characters at the species level in *Arichlidon* are therefore very conservative. This has been observed by the author in a number of other chrysopetalid genera. However, the small differences seen are usually very consistent, as the great number and range of material examined and whole specimens dissected, illustrates.

Table 1 shows that the majority of *A. hanneloreae* specimens possess lower rib counts of the lateral and main paleae compared to *A. reyssi*. Exceptions are certain specimens from offshore Western Australia (NW Shelf and Rowley Shoals) that possess comparatively high rib numbers of lateral, main and median paleae. An eastern Australian coastal specimen (Gladstone, Queensland) has similar high median and main paleae rib counts.

It has also been observed in *Arichlidon hanneloreae* that individuals from coral reefs often have main paleae with broader 'shoulders' and more sunken apices (compare Figs 6A-B with 6C-D).

Epitokous setae. Two benthic specimens of *Arichlidon hanneloreae* possess accessory neurosetae that originate from a position just below the ventral acicula, i.e. superior to the normal set of neurosetal types. These fine setae are composed of slender shafts that are internally dissected with horizontal striae, poorly chitinized homogomph joints and long, slender spinigerous articles (Fig. 3J). Overall they are longer than the normal neurosetae and are present in most body segments eg. epitokous setae number from five per parapodium until the posterior seven segments of the posterior body specimen from Gove (NTM W.13026) and up to 14 per parapodium from segment 14 to 38 in the 43 segment entire specimen from Gladstone (QM GH 615).

Both these specimens are ovigerous females with mature egg 'packets' measuring 0.04-0.06 mm across and individual units inside 0.0045 mm (Figs 3A-B). *Arichlidon* is known to possess planktonic larvae which have been collected and described from coastal embayments (Cazaux 1968 as *C. debile*; Watson Russell 1987). Gametogenic adults with accessory neurosetae of an

Table 1. Comparison of setal types (mid-body) within and between *Arichlidon* species.

Locality	Reg. no.	No. segments entire	No. lateral paleae	No. ribs lateral paleae	No. median paleae	No. ribs median paleae	No. ribs main includ. subunit 1 palea	Species
Bass Strait	NMV F82,902	21	4-6	8-14	5	7-13	14-16	<i>A. hanneloreae</i>
Middleton Reef	AM W23370	48	5-7	7-15	5	8-14	14-16	"
Gladstone	QM GH 615	43	4-6	7-14	5	8-16	14-17	"
Townsville	NTM W1563	33	4-5	6-14	5	8-13	14-15	"
Lizard Is.	NTM W13191	52	4-6	6-13	5	7-14	14-16	"
Madang	NTM W7574	42	5-6	8-15	4-5	8-13	14-16	"
Darwin Harbour	NTM W. 2052	22	5-6	6-14	4-5	9-15	16-18	"
NW Shelf	NTM W13199	40	5-7	7-15(17)	5	9-16(17)	15-17(19)	"
Ashmore Reef	NTM W9304	53	5	7-14	5	9-16	14-16	"
Sumatra	USNM 45381	45	4-6	8-14	5	9-15	14-16	"
Marshall Is.	LACM n10164	Mid body segs	5-6	8-15	4-5	9-14	14-15	"
North of Hinchinbrook Is.	AM W23347	38	5-7	6-16	5	9-16	16-18	<i>A. acropetalon</i>
Cape Verde Is.	NTM W13190	37	4-5	8-15(17)	4-5	9-17	14-16(19)	<i>A. reysyi</i>
Spain	NTM W2590	41	4-6	8-15(16)	4-5	9-15(17)	14-16(17)	"
E. Mediterranean.	SMF 5002	51	4-6(7)	9-15	4-5	10-16	14-17(18)	"

undescribed American *Arichlidon* species have also been collected from the plankton.

Divergence from the normal type most commonly relates to sexual maturity and the acquisition of epitokous swimming setae, especially capillary setae, is seen in gametogenic adults from a number of other polychaete families (Schroeder and Hermans 1975). This is the first observation of epitokous setae found in benthic and planktonic individuals within the Chrysopetalidae.

Distribution and habitat. *Arichlidon hanneloreae* is found in the warm waters of Australia, South east Asia and Papua New Guinea between 31° S and the Equator (Fig. 7). It has also been recorded from the Marshall Islands in the western Pacific. In this study *Arichlidon hanneloreae* has been predominantly recorded from Australian offshore coral islands, reefs, atolls and volcanic submerged sea mounts as far west as Ashmore Reefs and Rowley Shoals, Western Australia to Middleton Reef and Lord Howe Island, Tasman Sea, eastern Australia.

In areas where there has been intensive collecting the species occurs in moderate numbers over a wide range of coral habitats, eg. Lizard Is. northern Great Barrier Reef, from protected reefs in lagoons to pristine reefs in clear, deep waters of the outer barrier. Hutchings and Murray's (1982) study of recruitment of polychaetes to dead coral substrates showed that chrysopetalid taxa, of which *Arichlidon hanneloreae* made up a sizeable part, constituted fourth of the seven most dominant taxa. Large numbers settled preferentially to older blocks at the windward side between January and April, suggesting summer recruitment by planktonic larvae at a site exposed to the SE trade winds.

Arichlidon hanneloreae has also been recorded from coastal locations of Queensland and the Northern Territory in bays and harbours from more turbid waters. Where benthic studies have been carried out, the species has been found in consistently moderate numbers from a range of habitats eg. from silt, fine and coarse sand, gravel and shell from Darwin Harbour and Melville Bay, Gove in dry and wet seasons.

It is known that the south-eastern coast of Australia receives periodic surface currents from Great Barrier Reef waters (Veron 1974) and therefore offers potential sites for settlement of planktonic larvae of tropical polychaete species. As *Arichlidon* species have been recorded as possessing such larvae, the presence of a single specimen of *Arichlidon hanneloreae* from a large benthic survey in the temperate waters of Bass Strait, Victoria is not surprising.

Etymology. This species is named in honour of Hannelore Paxton, who influenced my decision to work in polychaete taxonomy.

Arichlidon acropetalon sp. nov.
(Figs 5A-B; 6E-F)

Type material. HOLOTYPE - Australia, Queensland, North of Hinchinbrook Island, 18° 11' 01" S, 147° 25' 50" E, Stn. 22, 490-472 m, sled, coll. *RV Franklin*, 26 August 1988, 1 specimen, female with eggs, AM W23347.

Description. Holotype entire 38 segments; length 5.6 mm, width 1.00 mm. Prostomium with long palps, long subulate median and lateral antenna visible in ventral view. Mid body setigers with notosetae comprising five to seven lateral paleae; outer two with 6-11 (rarely 12) ribs, inner group with 13-15 (rarely 16) ribs of which four to five finely raised (Fig. 5A). Main paleae number 13-15 with 16-18 ribs including four to seven raised ribs of which three to four extend full length of palea. Most medial main palea (subunit 1) very slightly asymmetrical with 16-18 ribs and five raised ribs. Median paleae number five; inner two with 9-12 ribs, outer group with 13-16 ribs; tallest median palea with 15-16 ribs, second tallest median palea with 15-16 ribs (Fig. 5B). Subunit 2 symmetrical median palea with 9-10 ribs of which two to three finely raised. Lateral, main and median paleae with elevated distal ends, distinct pointed apices, rounded shoulders, fine serrate margins; granulation absent (Fig. 6E-F).

Neurosetal types as for *A. hanneloreae*; ventral cirri long, very slender. Pygidium slightly damaged; with ventral cone, anal cirri not visible.

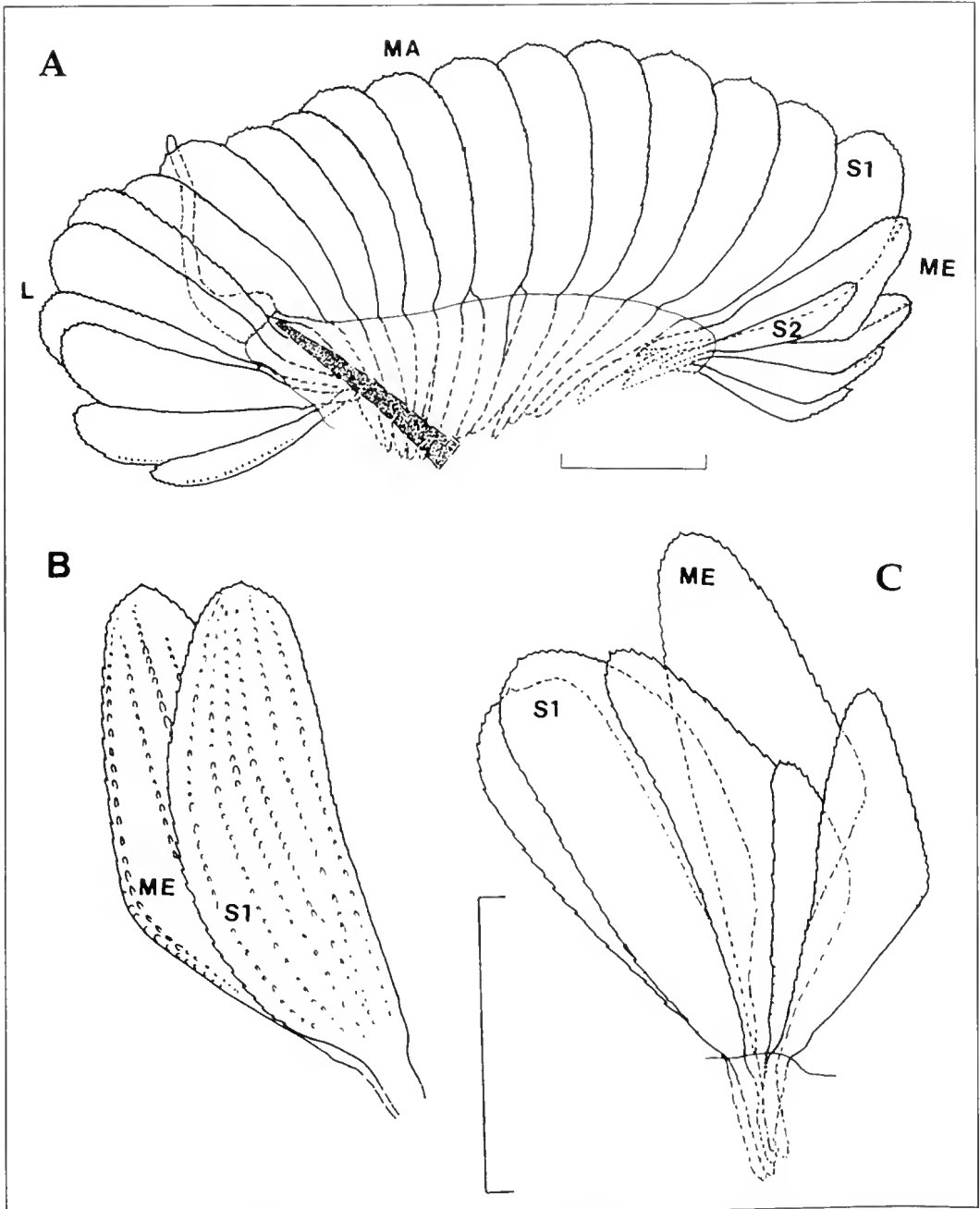


Fig. 4. A. *Arichlidon hamneloreae*, NTM W1564, notopodium, segment 15, anterior view; B. *A. hamneloreae*, NTM W13092, notopodium in part, segment 19, anterior view; C. *A. reyssei*, NTM W2590, notopodium in part, segment 19, anterior view. Abbreviations as for Figure 1. Scale = 0.1 mm.

Remarks. Considering the morphological conservatism of *Arichlidon* species over a large area and depth gradient it was perplexing to find a mature specimen from moderately deep waters off the Queensland

coast that differed quite markedly from the *A. hamneloreae* type.

Paleae types of *A. acropetalon* possess distinctly rounded 'shoulders' and highly elevated apices lacking granules which

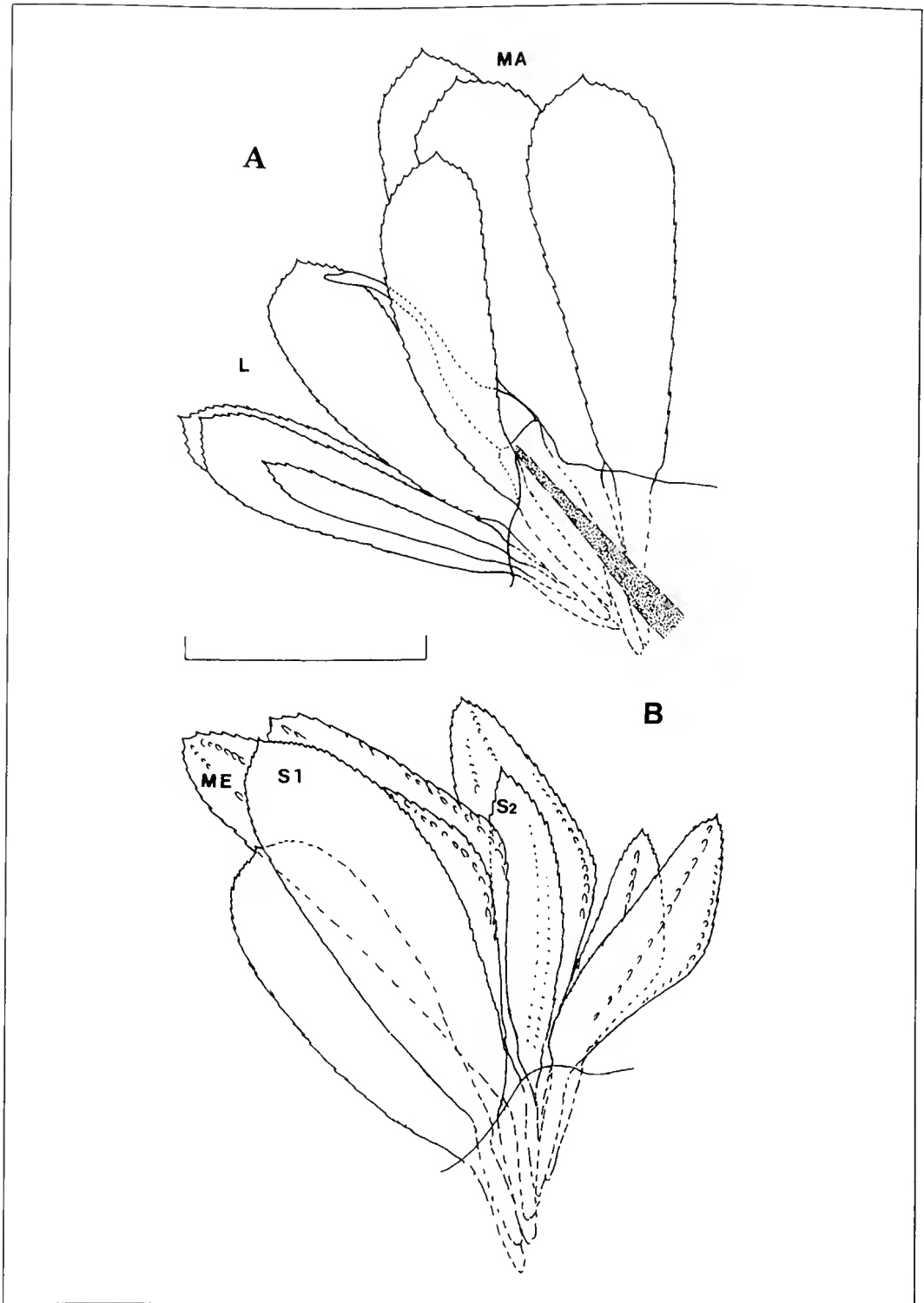


Fig. 5. *Arichlidon acropetalon*, AM W23347. **A, B**, notopodium in lateral and medial parts, segment 15, anterior view. Abbreviations as for Figure 1. Scale = 0.1 mm.

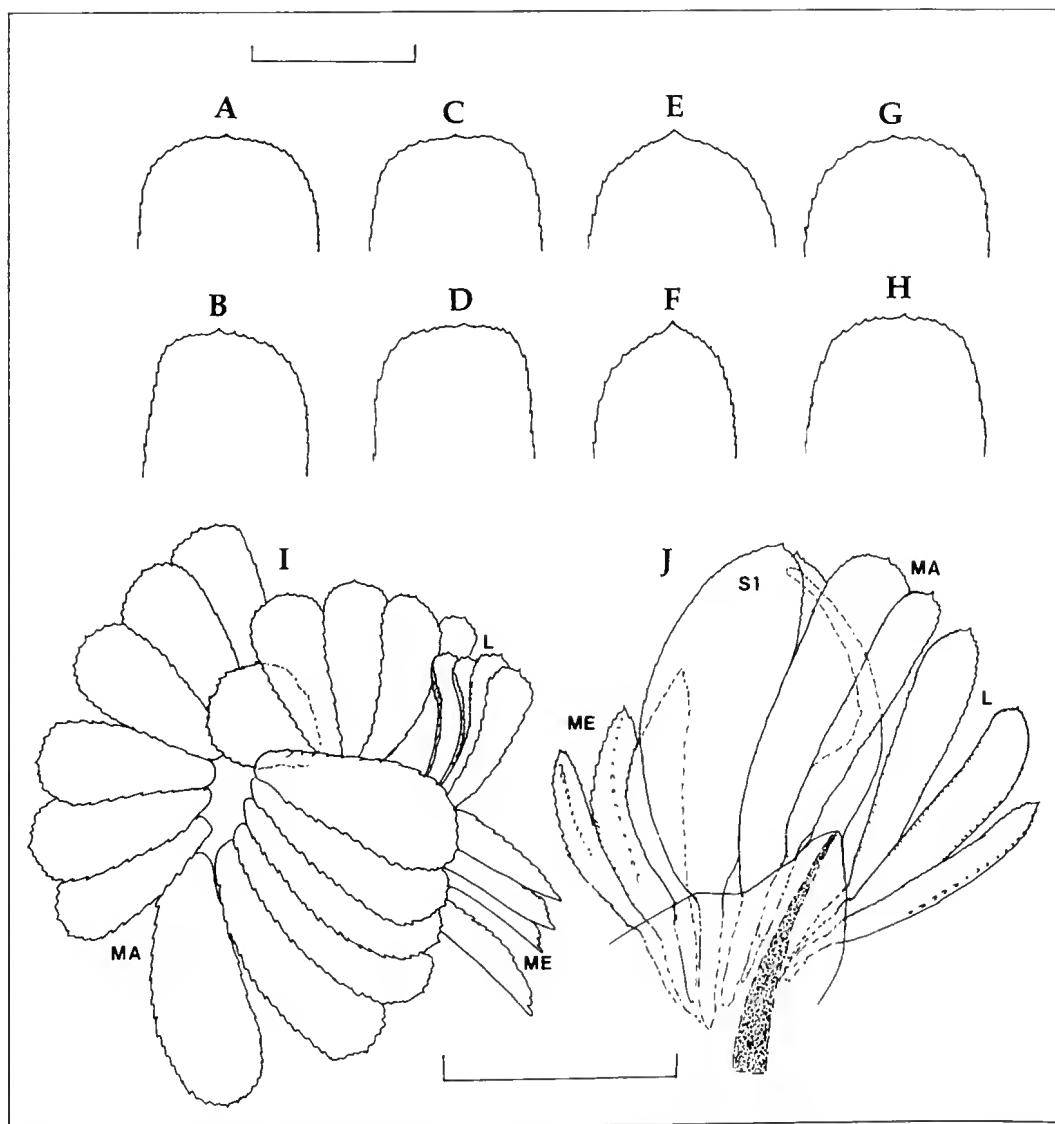


Fig. 6. Comparative paleae shapes. Each pair represents a mid main palea (eg. A) and the medial-most tallest lateral palea (eg. B). Scale for a-h = 0.04 mm. **A, B.** *A. hanneloreae*, Townsville, Queensland, sediment, 2 m; **C, D.** *A. hanneloreae*, Cooks Passage, Great Barrier Reef, coral rubble, 10 m; **E, F.** *A. acropetalon*, north of Hinchinbrook Is., Queensland, 490 m; **G, H.** *A. reyssi*, Mar de Alboran, Spain, Mediterranean, coralline algae, 55 m; **I.** *A. hanneloreae*, NTM W21319, notopodium, segment 3; **J.** notopodium segment 51. Scale for I-J = 0.1 mm. Abbreviations as for Figure 1.

separates it from *A. hanneloreae* and *A. reyssi*. Mid-body segments have consistently higher numbers of paleae types and ribs in the lateral, main and median groups compared to *A. hanneloreae* (with a few exceptions, see Table 1). The subunit 1 palea is noticeably more slender than in *A. hanneloreae* and the subunit 2 palea is

broader with 10-12 ribs rather than the customary seven to nine ribs (Fig. 5B). The ventral cirri are more slender than those seen in the other two species.

It also differs from *A. hanneloreae* and is similar to *A. reyssi* in possessing the lateral-most median palea as being the tallest palea in the fan in mid body segments (Fig. 5B).

Etymology. The species name *acropetalon* is from the Greek; *acro* meaning 'peak' and *petalon* 'leaf' and refers to the raised apices of the paleae. Gender neuter.

***Arichlidon reyssi* (Katzmann, Laubier and Ramos, 1974) new combination**
(Figs 4C, 6G-I)

Bhawania reyssi Katzmann, Laubier and Ramos, 1974: 313-317, fig. 1a-g. Type locality the Adriatic.

New genus new species 1 - Watson Russell 1986: 156; 1987: 660-670; 1991: 293.

Paleanotus heteroseta Rullier, 1964: 142-3.

Bhawania goodei Rosenfeldt, 1989: 219.

Chrysopetalum debile Cazaux, 1968: 536-541, figs 8, 9 (larvae).

Type material. HOLOTYPE - Adriatic Sea, 43° 41.3' N, 15° 44.2' E, 51 m, NMW 13222, coll. W. Katzmann; 35 segments, 3.8 mm length, 0.7 mm width, specimen in 2 halves. PARATYPES-locality as above, 24 segments, 2.2 mm length, 0.8 mm width; 31 segments, 2 mm length, 0.9 mm width, NMW 13222.

Additional material. MEDITERRANEAN, Spain, Mar de Alboran, from *Corallium rubrum* bottom, 40-55 m, coll. G. San Martin. 2, NTM W2590; eastern Mediterranean, 32° 54' N 31° 53.70' E - 32° 55' N 31° 52.61' E, Stn. 25 Ku, sandy mud with shell debris, 196-199 m, coll. *Meteor*, 1 June 1993, 77, SMF 5002, (largest specimen 50 segments, 4.8 mm length, 1.4 mm width; smallest 13 segments, 1.3 mm length, 0.7 mm width); same locality and details, 5, NTM W13180; 34° 45.25' N 25° 52.31' E - 34° 44.14' N, 25° 50.89' E, Stn. 18, soupy mud, 1386-1386 m, coll. *Meteor*, 26 May 1993, 1, SMF 5004; 36° 35.69' N 21° 31.95' E - 36° 37.68' N 21° 30.37' E, Stn. 16 Ku, soupy mud, 3832-3947 m, coll. *Meteor*, 22 May 1993, 1, SMF 5001; Egypt, Sinai, Katib el Galls, Stn. SLM 778-27VI-91, 121 m, 4 February 1968, 1 fragment, HUI POLY220. EASTERN ATLANTIC, Cape Verde Islands, SW of Maio, 15° 06' N, 23° 13' W, 75 m, coll. H. Ten Hove, CANCAP expedition, 25 August

1986, 5, NTM W13190; west coast Brava Island, from red sponge, Stn. 52, rock, 20 m, coll. *Calypso*, 21 November 1959, 1, MNHN A488; 15° 26.5' N, 23° 14' W, between Maio Is. and Boavista Is., Stn. 64, shelly bottom, 100 m, coll. *Calypso*, 24 November 1959, 2, MNHN A393. RED SEA; Stn. SO-02/27TA, 757 m, MESEDA I Expedition, 16 October 1977, 1, SMF 3783; 13° 39.30' N, 42° 43' E, inside dead *Atys* shell, coll. John Murray Expedition 1933-4, 1 on slide, BMNH 1938.7.29.1; Egypt, Mission R. Pd. Dollfus, 15 December 1929, 1, MNHN A360.

Description. Holotype entire 35 segments. Anterior segments relaxed. Subulate median antenna visible on anterior edge of prostomium; two pairs of eyes visible above nuchal fold; two long cylindrical palps visible ventrally. Segment 2 with six short paleae with 12-14 ribs. Subsequent body segments with notosetae comprising four to six (seven) lateral paleae; outer group with 7-12 ribs, inner group with 12-16 (17) ribs. Main paleae number 10-14 with 14-19 ribs, four to seven raised ribs (three to four extending full length of palea). Most proximal main palea (subunit 1) slightly asymmetrical with 16-18 ribs and five raised ribs, present from 15th segment and continuing to posteriormost segment. Median paleae number three to five (two counts of six only on segment 3); medial group with 9-13 ribs, lateral group with 11-16 (18) ribs. Lateral-most median palea with 15-17 (18) ribs present about segment 5 to 6, continuing as tallest palea in entire paleae fan (Fig. 4C); within posterior 10 setigers becoming same height then shorter than paleae of main fan. Subunit 2, symmetrical, slim median palea with seven to nine ribs including two lightly raised ribs; present mid body, continuing to end of body (not always present on all posterior segments, often difficult to see). Main paleae broad with raised small apices, strong serrate margins, heavily ornamented raised ribs, dense to lighter granulation on superior palea surface (Fig. 6G-J).

Neurosetae comprising superior group of one to two spinigers with long slim shafts and attenuated blades; one extra or replacement short spiniger present within

posterior setigers. Mid superior group comprising two (three to four on anterior setigers) long bladed falcigers in upper position and four to eight (10 anteriorly) medium length bladed falcigers below; both types with strong basally dentate blades. Mid inferior group of 6-10 falcigers with shorter broader blades. Inferior group of 6-10 falcigers with short broad blades.

Pygidium composed of slender ventral cone, one anal cirrus present (one broken) on dorsal pygidial structure.

Remarks. The distinguishing character of *Arichlidon reysi*, the tall lateral-most median palea, is evident in mid-body segments in the majority of material examined, which separates it from the Australian species *A. hanneloreae*. In a mature dissected *A. reysi* individual of 42 segments, this character is clearly present from setiger 5 to 35 and in the

holotype from setiger 5 to 30 of 34 segments entire (Fig. 4C).

The MNHN Cape Verde specimens consisted of small fragments that recognisably belonged to *A. reysi* as did the numerous specimens collected by the CANCAP Expedition, eg. forty two individuals from Stn. 7.047.

Abyssal depth material from the eastern Mediterranean did not differ markedly from those examined from the inter and sub-tidal depths of the Mediterranean and Adriatic. The tall lateral-most median palea, while present throughout the majority of segments within an individual, was at times absent. A juvenile specimen of 13 segments (SMF 5004) had a few tall median paleae present in the mid posterior body, although it came from the same collection as distinct *A. reysi* adults.

Examination of *Arichlidon* material,

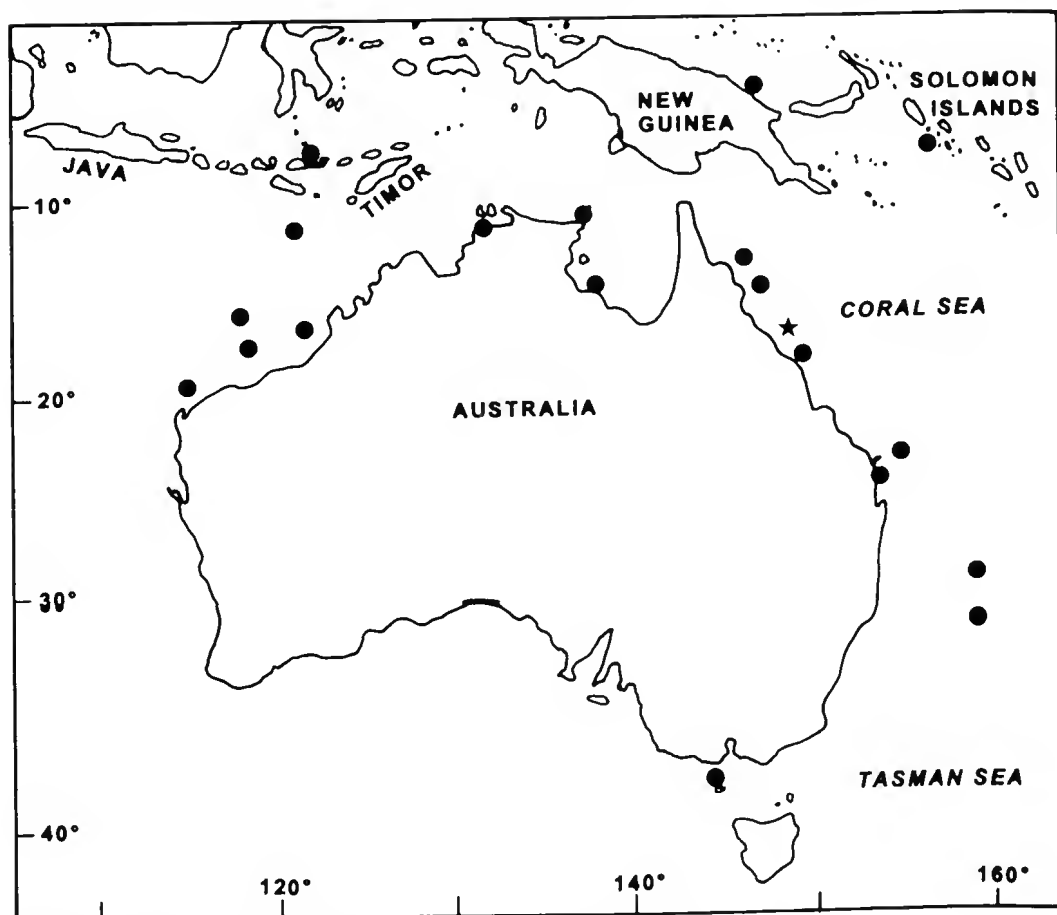


Fig. 7. Distribution map of *Arichlidon* species. Dot: *A. hanneloreae*. Star: *A. acropetalon*.

collected south of the Mediterranean from the Red Sea and Egypt, similarly contained specimens in which the tall lateral-most median palca of mid body segments were present or absent.

Distribution and habitat. The distribution of *A. reyssi* ranges from the Cape Verde Islands, NE Atlantic to the Mediterranean and Red Sea.

This species has been quite commonly collected from the Cape Verde Islands, from coarse sand, shell, rock and calcareous algae substrates in depths from 20 to 425 m. The marine fauna of the Cape Verde Islands represents West African species, American elements absent from the continental African plateau, small numbers of endemic species and the southern limit of east Atlantic and Mediterranean species (Rullier 1964); *A. reyssi* may belong to the last category.

Mediterranean material can be found from intertidal hard substrates to sandy muds with shell debris (199 m) and the beige brown soupy muds at 3947 m at sites in the eastern Mediterranean. These deep water stations have higher salinities than normal, ranging from 38.24‰ at Stn. 13Ku to 38.60‰ at Stn. 25Ku. Temperatures in the Levant Basin are also relatively warmer, ranging from 12.9° C at 862 m, 13.6° C at 3,947 m to 15.6° C at 199m. The Mediterranean is characterized by homothermy below ca. 200 m (Dieter Fiege pers. comm.).

Red Sea specimens range from intertidal to 757 m.

ACKNOWLEDGMENTS

I am grateful to the following people for the loan of material: Nechama Ben Eliahu (HUJ), Kristian Fauchald (USNM), Jeanne Renaud-Mornant (MNHN), Pat Hutchings (AM), E. Kritscher (NMW), Pat Mather (QM), Alex Muir (BMNH), Robin Wilson (NMV) and Susan Williams (LACM). Dieter Fiege (SMF) kindly lent material from the deep waters of the Eastern Mediterranean and Harry Ten Hove (ZMA) lent specimens from the Cape Verde Islands.

I would especially like to thank Guillermo San Martin for the gift of specimens from

the Spanish Mediterranean coast and the Caribbean, and Thomas Perkins for his notes on material from Florida waters and the loan of planktonic adult specimens. I also would like to thank Sue Doyle at the SEM unit, Macquarie University, Sydney, for help with the SEM micrographs, anonymous reviewers for critically reading the manuscript and the Northern Territory Museum for funds to complete an earlier part of this study.

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Accepted 30 June 1998

Book Review

Body and Soul: an Aboriginal view

Anthony Rex Peile S.A.C.

Edited by Peter Bindon

1997

Hesperian Press

65 Oats Street,

Carlisle W.A. 6101, Australia,

and

The Pallottines in Australia

60 Fifth Avenue,

Rossmoyne, W.A. 6148, Australia.

i-xxvi, 308 pp. Hardcover \$50

Aust. ISBN 0 85905 233 8.

To have known Fr. Anthony Peile was to have known that all too rare being, in this age of short term achievements: a man with a quest. Fr. Peile had made it his life's work to seek out, digest and present the physiological and metaphysical concepts of self from the perspective of the Kukatja, a people who had their homelands about the common border of the Great Sandy and Tanami Deserts.

For the twenty-eight years he was resident at Balgo Hills Pallottine Mission, in the south-east Kimberley, Fr. Peile honed his fluency in Kukatja, Walmajarri and Pintupi, the main languages spoken by the Aboriginal people of Balgo. Not content with the more mundane levels of language acquisition, Fr. Peile delved into the arcane knowledge and language that bound human physiology to a deeper philosophical rationale, and he perceived that this required understanding if there was going to be a positive result in the delivery of Western health care systems to the Aboriginal clientele resident at Balgo.

At the Kukatja Research Centre that he set up at Balgo, Fr. Peile amassed a vast database of linguistic and ethnographic information focusing particularly on Western Desert health and medicine, ethnoherpetology and ethnobotany. Nine papers were produced on these various topics, one of which (Wiminytji and Peile 1978) was co-authored by one of his most senior informants, the

well known Balgo artist and 'Clever-man' Wiminytji Tjapangarti. Other draft manuscripts or materials prepared by Fr. Peile have been produced, subsequent to his death, by other scholars or are in the process of publication (e.g. Valiquette 1993). Within the files and records left by Fr. Peile is a legacy of cultural information available to both the future generations of Kukatja, Pintupi, Ngarti and Walmajarri at Balgo, and future scholars who, it is hoped, will build on and develop this valuable resource to the benefit of the Aboriginal people of the northern Western Desert. For a long time, scholars and health practitioners, who have been aware of the existence of Fr. Peile's huge manuscript that forms the basis for *Body and Soul: an Aboriginal View*, have been anxiously awaiting publication of this most valuable document.

Body and soul: an Aboriginal View is a detailed journey into human physiology and its concomitant metaphysical rationale from the perspective of the Kukatja. Each chapter contains not merely details or concepts dealing with esoteric and mundane ethnographica, but also a stated understanding of the importance of these data in achieving a positive result in the delivery of cross-cultural health services. The first chapter outlines the Kukatja life cycle. Chapters 2-4 deal with human anatomy, addressing in detail both internal and external structures, organs and secretions. Kukatja concepts of the functional bodily processes - ingestion, digestion, respiration, reproduction, sleeping and dreams, and emotions are covered in detail in Chapter 5. Chapters 6 and 7 cover topics of Health and sickness and the Treatment of sickness respectively, providing rationales which allow the cross-cultural worker to appreciate attitudes of Aboriginal patients to both afflictions and the healing process. Finally, Chapters 8 and 9 deal with biological agents in relation to health issues. Chapter 8 includes significant sections on the deleterious impacts arthropods may have on human beings and

the medicinal use of insects. The properties of animal fats are discussed and there is a brief section on the medicinal properties of rabbits - Kukatja country being at the extreme northern margin of that animal's range. Chapter 9, while focusing on ethnobotany, includes sections on the use of smoke and steam or vapour, bush tobacco and, paradoxically, ochres in the healing process. Finally there is a brief chapter on drowning and resuscitation.

The body of text is supported by a thirty-five page glossary of Kukatja terms relating to health, physiology, ethnobotany and ethnozoology. A thirty-five page bibliography details all references mentioned in the text.

The strength of this book lies not in its linguistic or theoretical content, but in the vast amount of ethnographic detail that he has amassed and organised. In his writing, Fr. Peile approached the vast topic he had selected from a rather archaic stance, and the politically correct may take exception to some of the idiom employed. Hasty condemnation, however, must be avoided by the hypercritical. To the Kukatja and other Aboriginal people at Balgo, Malan, and adjacent centres and outstations, Fr Peile was a friend, confidante, a learned and concerned man and a priest. As one, aware also of the vast repository of cultural information that Fr. Peile had amassed, who had seen him working with his close Kukatja friends in documenting so many aspects of their culture as well as conducting his Pastoral duties (in fluent Kukatja), I know that this posthumous publication would have provided him with deep satisfaction.

The editor, in preparing Fr. Peile's original 550 plus pages of manuscript for publication, faced the unenviable situation of carefully pruning an unwieldy yet immensely important body of information down to manageable size without destroying the integrity of either the subject matter or the author's intent. Peter Bindon is to be congratulated on the final product.

Hesperian Press and the Order of Pallottines in Australia are also to be commended for ensuring that Fr. Peile's work no longer runs the risk of being consigned to obscurity.

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GUIDE TO AUTHORS

Authors are advised to follow the layout and style in the most recent issue of *The Beagle*. A comprehensive style guide is available on request.

Three copies of typewritten manuscripts should be submitted. Manuscripts should be in English, double-spaced throughout and have a margin of at least 4cm on the left hand side. Text should be on one side of good quality A4 bond paper. If available, a computer file of the manuscript (on 3 1/4" MS/IBM DOS floppy disk) should be submitted together with the printed version. Where appropriate, articles should conform to the sequence: Title, Abstract, Keywords, Introduction, Materials and Methods, Text, Discussion, Acknowledgments, References.

The Title should be concise and informative. An abridged title (not exceeding 50 letter spaces) may be nominated for use as a running head.

The Abstract should not exceed 150 words, and should state concisely the scope of the work and give the principal findings.

Keywords, to facilitate information retrieval, of up to 15 in number should be chosen to outline the main subjects covered.

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Systematic papers must conform with the International Code of Zoological Nomenclature and, where ever possible, with their recommendations.

Synonymies should be given in the short form (*taxon* author, date: page) and the full reference cited at the end of the paper. Full citations of taxa used in the text (i.e. *taxon* author, date) must also be included in the references, whereas the short citation (i.e. *taxon* author) need not be included. Subsequent citations of taxa given in synonymies should be separated from bibliographical details by a dash (-).

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The Beagle

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